VANCOUVER ISLAND
ROOSEVELT ELK/
INTENSIVE FORESTRY
INTERACTIONS

PHASE 1 (1981-1986)
JOB COMPLETION REPORT

INTEGRATED WILDLIFE INTENSIVE FORESTRY RESEARCH

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VANCOUVER ISLAND ROOSEVELT ELK/ INTENSIVE FORESTRY INTERACTIONS

Phase 1 (1981-1986)
Job Completion Report

K.R. Brunt, D.Q. Becker, and J.A. Youds

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SUMMARY

Roosevelt elk *(Cervus elaphus roosevelti)* were studied near Campbell River, on northern Vancouver Island, from April 1981 until March 1986. Thirty-three elk were radio-collared, including 24 adult cows, 2 yearling bulls, 5 adult bulls, and 2 calves. Both migratory and non-migratory movement patterns were exhibited. Annual home range sizes of migratory elk were approximately 6 times larger than those of non-migratory elk. Densities on annual ranges of both migratory and non-migratory elk varied from 0.6 to 3.0 elk per km². Densities on seasonal ranges (winter and summer) of migratory elk ranged from 3.0 to 6.5 elk per km².

Elk diets varied by season: spring diets were dominated by shrubs, ferns, and graminoids; summer diets contained high proportions of shrubs and half shrubs; fall diets showed a shift to ferns and conifers; and winter diets were dominated by graminoids, conifers, and ferns. Use/availability comparisons indicated that deer fern (*Blechnum spicant*), grasses, twinflower (*Linnaea borealis*), western hemlock (*Tsuga heterophylla*), and sedges (*Carex* spp.) were the preferred plant taxa during the mild winters of 1982/83 and 1983/84. Moderate winter diets were dominated by deer fern, sword fern (*Polystichum munitum*), western hemlock, western redcedar (*Thuja plicata*), and huckleberries (*Vaccinium* spp.).

Animal condition indices collected during the study indicated that elk were on a relatively high nutritional plane during all seasons. Estimated dietary crude protein levels ranged from 8.0% in winter to 17.5% in summer. Diet dry matter digestibility ranged from 45% in winter to 59% in summer.

Summer calf:cow ratios in two migratory herds averaged 48 calves per 100 cows. Spring calf:cow ratios from these two herds averaged 41 calves per 100 cows and were negatively correlated with winter severity ($p<.005$).

A pregnancy rate of 85% for cows 2.5 years of age and older was calculated for the study area and adjacent areas. Mean conception and parturition dates were September 28 and June 2, respectively. Hunting (legal and illegal), wolf predation, and over-winter mortality were the major factors regulating population levels. Analyses indicated that elk populations within the study area and adjacent areas are generally increasing.

The majority of calving sites occurred on the summer range, and seven of the nine occurred in second growth. Minimal slope and adequate security cover appeared to be the primary factors affecting calving site selection. The effects of logging activities on calving habitat use remains unclear.

Elk habitat use assessments during summer indicated a preference for bogs and deciduous stands. There was high use of old-growth (38%) and 0- to 20-year-

old second-growth (34%) stands on the summer range, though these stand types were used only in proportion to availability.

During two mild winters (1982/83 and 1983/84), elk displayed a preference for bogs, deciduous-conifer complexes, and 20- to 60-year-old second-growth with moister ecosystem associations. A multiple regression model incorporating four habitat variables (mean percent cover of sedges, mean percent cover of grasses, canopy closure, and mean percent cover [below 2 m] of western hemlock) was significant ($p<.025$) and explained 95% of the variation in stand type preference. Within stand types, elk selected moister ecosystem associations (*Blechnum*, *Polystichum-Achlys*, and *Rubus spectabilis*) and avoided the drier ecosystem associations (*Gaultheria* and *Rhacomitrium*-lichen). Home range sizes during the mild winters decreased as the proportion of bogs and deciduous-conifer complexes within the home range increased, suggesting a relationship between the carrying capacity of a winter range during a mild winter and the abundance of these habitat components.

During a moderately severe winter (1984/85), elk displayed a preference for rock outcrops, deciduous-conifer complexes, and 21- to 60-year-old second-growth with moister ecosystem associations. The availability of grasses and sword fern explained 95% of the variation in stand selection throughout the entire winter. Snow depth influenced the availability of preferred forage species which in turn influenced elk habitat use patterns. During snow accumulation periods, home range size decreased as the proportion of rock outcrops, deciduous-conifer complexes, and 21- to 60-year-old second-growth with moister ecosystem associations in the home range increased, suggesting a relationship between the carrying capacity of a winter range during a moderately severe winter and the abundance of these habitat components.

Winter activity monitoring indicated peaks in activity at daylight and dusk. A daily forage requirement of 6-11 kg dry matter during a mild winter was estimated.

Elk displayed a high preference for edges between open areas and cover at all times. On summer ranges, 95% of locations in openings were within 200 m of cover; on winter ranges, 80% of locations in cover were within 200 m of openings. It is recommended that elk use of an area will be encouraged if an edge between open and cover habitats is maintained within 200 m of any point on all seasonal ranges.

All forest management activities within or adjacent to elk seasonal ranges have the potential to affect elk habitat use patterns and population performance significantly. Visual screens of vegetation around open areas that are heavily used by elk help to maintain elk use of these sites. Site conversion of stands from a deciduous to a coniferous dominated overstory may lead to changes in habitat use patterns of elk and may result in browsing

damage to regenerating conifers, especially if herbicides are used to reduce competition between conifers and elk forage species. Debris in backlog spaced stands excluded elk access to these areas and some form of debris treatment is required to encourage elk use in these stands.

Information is lacking on elk habitat use patterns and population performance during a severe winter in the absence of old growth. Other research needs and planned activities are identified.

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1.0 INTRODUCTION

Roosevelt elk (*Cervus elaphus roosevelti*) on Vancouver Island are a highly prized species for hunters and non-consumptive users alike. In 1988, over 7000 hunters applied for 239 available permits to hunt elk on the Island, indicating that the current supply falls far short of the recreational demand for the species.

Successful management of elk on Vancouver Island depends upon the protection and provision of important elk habitats through integrated forest and wildlife habitat management. Knowledge about elk habitat needs and the impacts of intensive forest management practices on these needs is required for effective integrated management of both resources. This study was initiated in 1980 to provide such information. The project is part of the Integrated Wildlife-Intensive Forestry Research (IWIFR) program, a cooperative effort of the British Columbia Ministry of Environment and Ministry of Forests.

The general objective of the elk research project was to collect information on elk habitat use in immature forests, and to use this information in formulating forest management recommendations. The first part (Phase I) of the program ended in March 1986. This phase consisted mainly of research of elk habitat preferences and requirements. An additional 5 years (Phase II) has been approved for the IWIFR program. During this period, the elk project will test and refine elk habitat management recommendations, and transfer information obtained during Phase I to forest and wildlife habitat managers.

In the latter part of Phase I, efforts were concentrated on collecting habitat use data from radio-collared elk in the Greenstone migratory herd during winter. There were two reasons for this approach: (1) winter is considered to be the most stressful period for elk, and the availability of winter ranges that satisfy elk requirements can become critical, limiting elk populations during severe winters; and (2) the Greenstone herd spends the winter in an area of intensively managed second-growth forest where the influences of silvicultural treatments on elk could be examined.

This report presents analyses and ecological interpretations of data collected during Phase I of the IWIFR elk project (April 1981 - March 1986). Specific objectives during this period were to examine the effects of forest management activities on elk through assessments of:

- seasonal habitat use;
- food habits;
- migratory habits;
- animal condition; and
- population status.

2.0 STUDY AREA

The study area, approximately 30 X 40 km (1200 km²), is located northwest of the city of Campbell River on Vancouver Island, and includes the Salmon River watershed and the area bounded on the south by Campbell Lake and on the north by Highway 19 (Figure 1). The area consists of a low-elevation (0-500 m) rolling, coastal plain and a higher elevation (500-1200 m) inland mountain region. Diggle and Addison (1977) provide a detailed description of the geology, landforms, and soils of the area. Three biogeoclimatic zones - the Coastal Douglas-fir (CDF), the Coastal Western Hemlock (CWH), and the Mountain Hemlock (MH) - occur in the study area (Krajina 1965). The area is under two major forest tenures: the Sayward Provincial Forest (SPF) and Tree Farm License (TFL) #7, held by MacMillan Bloedel Ltd. (Menzies Bay Division).

The first logging in the area occurred in 1869 at Elk Bay on the east coast of Vancouver Island about 30 km north of Campbell River. Since then, logging has progressed from east to west across the coastal plain and into the higher elevation inland mountains where current logging activities are concentrated.

Extensive fires occurred in the study area in 1938 and 1951, burning 30 000 ha and 9000 ha, respectively. Reforestation of these areas was initiated in 1939.

The coastal plain is now dominated by 30- to 45-year-old second-growth stands of Douglas-fir (*Pseudotsuga menziesii*) and western hemlock (*Tsuga heterophylla*). These stands are typically 30-40 m in height and 35-45 cm dbh with a mean canopy closure of 80-95%. Very few small blocks of old-growth forest remain. In second-growth stands, an intensive program of backlog spacing was undertaken in 1976 to reduce the density of trees. In total, 8300 ha were spaced as of 1982. The debris from spacing was mostly left untreated, resulting in debris depths exceeding 2 m in certain areas.

The inland mountains are dominated by mature and old-growth conifer forest and young (0- to 20-year-old) second-growth stands. The current cut rate within the study area is approximately 900 ha annually.

There is little historical information available on elk populations within the study area. Although Fish and Wildlife Branch survey records date back to 1954, until the late 1960's, sampling effort for these surveys was low and inconsistent. Surveys during the early 1970's suggested the existence of four discrete herds including the lower Salmon herd, estimated at 50; the Greenstone herd, estimated at 100; the Grilse herd, estimated at a minimum of 50; and the Greybe herd, estimated at 30.[1] With the exception of the Grilse herd, which is now estimated at 120-130, these counts are similar to present estimates.

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[1]Janz, D.W. 1977. Roosevelt elk in the Sayward Forest. B.C. Ministry of Environment, Nanaimo, B.C. Unpublished report.

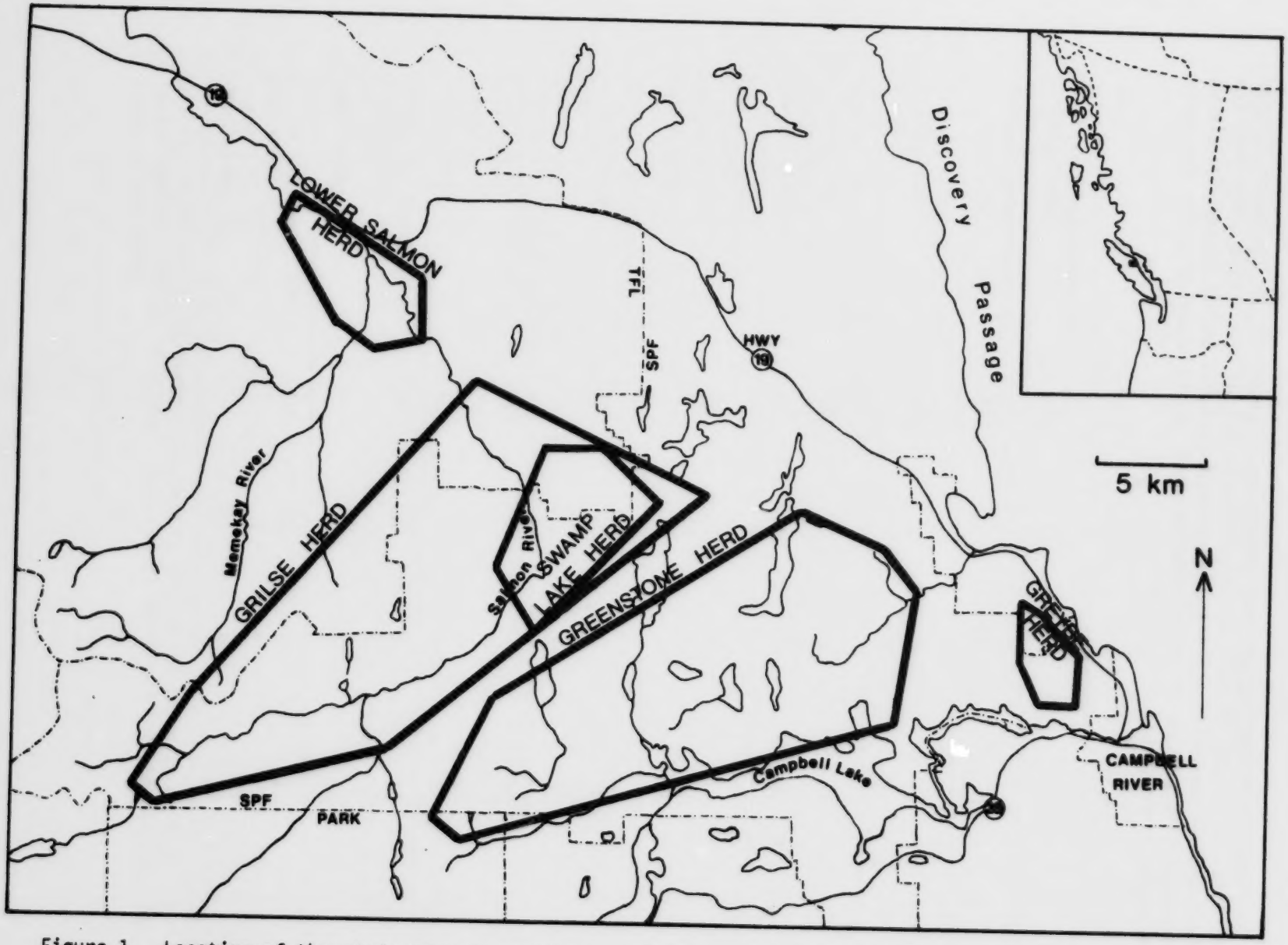


Figure 1. Location of the study area on northeastern Vancouver Island, showing the annual home ranges of study herds.

Prior to 1968, there was an open season on antlered elk on Vancouver Island, but this was closed in 1970 on the northern part of the Island (including the study area). In 1977, a limited entry hunt (L.E.H.) permit system for elk ws initiated. A summary of L.E.H. elk harvests in the study area for the years 1977-1985 is presented in Table 1.

Table 1. Limited Entry Hunt elk harvests in the study area: 1977-1985

Herd	Year	Antlered[1] elk		Antlerless elk	
		No. Permits Issued	No. Killed	No. Permits Issued	No. Killed
Grilse, Greenstone, and Swamp Lake	1977	10	8	10	7
Grilse, Greenstone, and Swamp Lake	1978	10	10	10	10
Grilse, Greenstone, and Swamp Lake	1979	10	7	10	6
Greybe's		5	2	--	--
Grilse, Greenstone, and Swamp Lake	1980	10	8	5	5
Greybe's		10	5	16	8
Lower Salmon		15	10	20	17
Grilse, Greenstone, and Swamp Lake	1981	10	8	5	4
Greybe's		10	5	16	11
Lower Salmon		15	8	20	7
Grilse, Greenstone, and Swamp Lake	1982	12	9	6	5
Greybe's		10	3	12	5
Lower Salmon		11	5	16	6
Grilse and Swamp Lake	1983	15	13	10	6
Greenstone		10	4	--	--
Greybe's		10	5	12	6
Lower Salmon		10	8	12	5
Grilse and Swamp Lake	1984	10	6	10	6
Greenstone		8	5	5	4
Greybe's		6	4	5	3
Lower Salmon		10	3	10	5
Grilse and Swamp Lake	1985	15	8	10	6
Greenstone		8	6	5	2
Greybe's		6	6	5	5
Lower Salmon		10	6	10	2

[1]Grilse, Greenstone, and Swamp Lake permits restricted to spike or 5 pt. or larger antlered bulls. Any adult bull can be harvested from the Greybe's or Lower Salmon herds.

3.0 METHODS

The primary focus of the study was to determine elk seasonal habitat preferences using radiotelemetry to assess habitat use/availability. In addition, assessments were made of elk winter activity patterns, diet content and quality, animal condition, and population characteristics.

3.1 Study Animal Capturing

3.1.1 Immobilizing

A total of 33 elk were immobilized between February 1981 and September 1984 by intramuscular (usually the rump or backstrap) injection of immobilizing drugs from a 4- or 5-cc dart. A Cap-Chur gun and green wad blanks (Palmer Chemical and Equipment Co. Inc., Douglasville, Georgia) were used to deliver the dart from a Bell 206B helicopter.

Two adult cows were immobilized with 10 mg etorphine hydrochloride and 40 mg acepromazine (Immobilon - Reckitt and Colman, Britain: etorphine 2.5 mg/ml, acepromazine 10 mg/ml). They were revived successfully with 12 mg of the antagonist diprenorphine (Revivon - Reckitt and Colman: diprenorphine 3 mg/ml).

The remaining elk (22 adult cows, two female calves, two yearling bulls, four 2.5-year-old bulls, and one mature bull) were immobilized with 78-108 mg fentanyl citrate in combination with 0-100 mg of xylazine (Rompun - Cutter Laboratories, Mississauga, Ontario: xylazine 100 mg/ml). Darts were "topped up" with distilled water to remove air pockets. Fentanyl citrate was mixed to a concentration of 30 mg/ml by dissolving a powdered form of the drug in a buffered solution (pH=4.1) of distilled water, lactic acid, and sodium hydroxide. The solution was stored at room temperature in a dark cupboard when not in use.

Most elk immobilized with fentanyl citrate were revived with 10-20 mg diprenorphine (either Revivon or M50-50 - Cyanamid Canada Ltd., Montreal, Quebec). Several required 30-32 mg of diprenorphine for full recovery and one adult bull required 56 mg.

3.1.2 Radio-collaring

All immobilized elk were fitted with configuration 5B radio transmitters (Telonics Inc. Mesa, Arizona) in the 150-151.3 MHz frequency range that had a rated operational life of 30 months. Most elk were also fitted with colour-coded ear tags for individual identification from visual observations. Radiocollars placed on all elk were very loosely fitted. During the summer, when long mane hair was not present, collars were observed to slide up and down an elk's neck as the head was lifted and lowered during feeding.

Radiocollars equipped with motion-sensitive devices were tightened slightly more to avoid this slipping. Collars fitted to immature elk were fitted to the same size as with adult animals to allow room for growth.

Two methods of attaching radiocollars to male elk were attempted to allow for growth and swelling of the neck during the breeding seasons. Five bulls (two yearlings, two 2.5-year-olds, and one mature bull) were fitted with collars that were modified with an automobile seat belt retractor, which would allow neck expansion and subsequent tightening of the collar. The remaining two bulls (both 2.5-year-olds) were fitted with collars with approximately 0.75 m of rubber surgical tubing protected by a length of fire hose.

3.1.3 Immobilized elk data collection

Various body measures, a blood sample, and a canine tooth for subsequent aging were obtained from most immobilized elk. Blood samples from 21 of the radio-collared elk were allowed to separate for several hours before the serum was removed, frozen (some for up to 10 months), and submitted for SMA-12 analysis. Island Medical Laboratories (Nanaimo, B.C.) analysed 15 samples. The remaining samples from four adult cows and two adult bulls were submitted to B.C. Bio Laboratories (Burnaby, B.C.), which also conducted progesterone level analyses for pregnancy detection in the adult cows. Teeth were sectioned and age estimated through cementum analysis by Matsons Laboratories, Mill Town, Montana.

3.2 Habitat Use Assessments

3.2.1 Habitat classification

Habitat types were classified on the basis of stand types and their associated ecosystem associations (Table 2). Ecosystem associations were identified by assessing site features (physiographic, soil, and vegetative characteristics) as described in Green et al. (1984). Stand types were delineated using forest cover maps and air photos.

The winter range of the Greenstone herd was stratified into habitat types with the use of 1:10 000 colour air photos, forest cover maps, and ground reconnaissance. Approximately fifteen 5 X 5 m permanently staked plots were subjectively placed in representative areas of each habitat type. Understory species abundance, canopy closure, soil characteristics (depth, texture, parent material, coarse fragment lithology, humus form and depth, and seepage), and topographic characteristics (slope position, percent slope, aspect, and elevation) were recorded for each plot. Abundance of understory species was visually estimated by percent cover. For tall shrubs and conifers below 2 m, percent coverage was estimated for two layers, 0-1 m and 1-2 m. Canopy closure was estimated with a spherical densiometer (Lemmon

Table 2. Stand type, ecosystem association and habitat type descriptions

Number		Description
Stand types		
1		Non-productive (forest land) - includes bogs and rock outcrops.
2		Deciduous-conifer complex - includes deciduous-conifer mixes and pure deciduous stands.
3		1- to 20-year-old conifer stands.
4		21- to 60-year-old conifer stands.
5		21- to 40-year-old *spaced* conifer stands - with 0.5 - 1.5 m debris depths.
6		Old-growth conifer stands (>200 years old).
Ecosystem associations[1]		
Very dry	.1	*Rhacomitrium* - Lichen spp.
	.2	*Gaultheria*
Moderately dry	.4	*Vaccinium* - Moss
	.5	Moss - *Mahonia*
Fresh (Moist)	.6	*Blechnum*
	.7	*Polystichum* - *Achlys*
Moist	.8	*Rubus spectabilis*
Wet	.9	*Sphagnum*
	.10	*Athyrium* - *Lysichitum*
Very Wet	.11	*Carex* - *Myrica* - *Spiraea*
Habitat types		

Habitat type = Stand type + ecosystem association(s)

e.g. Habitat type 4.5/.7 = a 21- to 60-year-old conifer stand with Moss - *Mahonia* as the dominant ecosystem association and a minor component of the *Polystichum* - *Achlys* ecosystem association.

[1]After Klinka *et al.* 1984.

1956). Four readings were averaged from each of the plot corners and the plot centre and mean plot values were then calculated from these five values.

Habitats on the summer range were stratified into stand types only, with the use of 1:10 000 colour air photos.

For calving sites, the following characteristics were measured or noted during 1983: elevation, percent slope, terrain, aspect, understory species, stand type, overstory height, overstory age, crown closure, distance to open water, distance to mature timber, distance to other vegetative cover, and a measure of hiding cover. Hiding cover characteristics of sites were measured with a 1.8 X 0.6 m vertically placed sighting tube (Leckenby *et al.* 1976). The proportion of the tube obscured was recorded as a percentage at 20-m intervals from the tube along the following six compass bearings: 0, 60, 120, 180, 240, and 300°. Measurements were taken in each direction until the tube completely disappeared from view. Information from calving sites identified in 1984 was obtained from 1:10 000 air photos.

3.2.2 Radiotelemetry

Radio-collared elk were located by remote triangulation from roads using a 3-element directional Yagi antenna and Telonics (Mesa, Arizona) receiving equipment, including a TR-2 receiver coupled with a TS-1 scanner/programmer and a TDP-2 digital data processor. Bearings on radio-collared elk were field plotted on forest cover maps or 1:10 000 air photos to determine from where subsequent bearings should be taken, and when a sufficiently precise location had been obtained. The accuracy of this method was tested through triangulation of randomly placed radio collars. These tests indicated that in relatively flat terrain, accuracy of the triangulation method was within 50 m of the actual location. In steep or rolling terrain, however, accuracy was reduced at times to within 100-400 m of the actual location. Radiolocations were not stratified by potential accuracy due to the influences of terrain but efforts were taken to obtain sufficient radiotelemetry bearings to minimize the triangulation error polygon. In most instances, radiolocation accuracy was considered to be within 50-100 m of the true location.

Most radio-collared elk were located approximately twice weekly from April 1981 through March 1982 and once monthly from April 1982 through October 1984.

Beginning in May 1982, certain adult female elk were selected and their locations monitored two to eight times daily for a period of 4 to 10 days. These intensive monitoring sessions were carried out in May, June, and July of 1982, January and February of 1983 and 1984, and November 1984 through March 1985.

During the calving season (May and June) of 1983 and 1984, cow elk in the Grilse Creek area were monitored up to four times daily to determine their calving sites. From mid-May to late June 1986, an employee of MacMillan Bloedel's Land Use Planning Advisory Team (LUPAT) worked in the Grilse Creek area to examine the influences of logging activity on calving site selection, using radiotelemetry and direct observation.

Distance to the nearest edge between forested habitats and open habitats (bogs, rock outcrops and 1- to 20-year-old conifer stands) of elk radiolocated in forested habitats on the Greenstone winter range was asessed from 1:10 000 colour air photos. Estimated distance to the nearest forest edge of elk in open habitats was assessed from visual observations on the Grilse summer range.

3.2.3 Home range and migration assessments

Annual home range and some seasonal home range sizes were assessed using the Home program (Harestad 1981). Fidelity of radio-collared animals to seasonal and annual ranges over the period of the study were used to identify separate herd ranges.

Seasonal home ranges of specific herds were delineated using the minimum area method (Mohr 1947) on 1:10 000 air photo mosaics. Availability of habitat components for specific herds on the different seasonal ranges was defined as the area encompassed by the outermost locations of radio-collared elk. A computer digitizer was used to determine sizes and proportions of habitat components within home ranges. This gave estimates of relative habitat availability for habitat selection indices.

3.2.4 Winter habitat use monitoring

Intensive monitoring sessions were carried out in the winters of 1982/83, 1983/84, and 1984/85 on radio-collared elk in the Greenstone herd. The herd's winter range was located in low elevation, intensively managed second-growth forests where the influence of silvicultural activities on elk habitat selection could be assessed.

Elk locations were monitored daily for sessions of 4 to 10 days while they were on the winter range from late November to early March. During mild winters (1982/83 and 1983/84), baseline data were collected on home range size, diet composition, habitat use, and forage availability in permanent plots in different habitat types on the winter range. In the moderate winter (1984/85), intensive monitoring sessions were initiated and continued throughout significant snowfall events. Criteria for significant snowfall events included an increase of 10 cm of snow at a low elevation snow station on the winter range or the entire period that snow depths exceeded 20 cm at this station. Intensive monitoring was discontinued when milder weather

conditions resulted in a 10-cm decrease in snow depth over 24 hours at the indicator station.

Outside intensive monitoring sessions, winter habitat use was assessed by daily radiolocations of as many elk as possible. These data were supplemented by walk-in assessments to identify the important factors of habitat use (either immediately after radiolocating a group of elk or the following day). Temporary plots (5 X 5 m) were placed in areas of use to assess forage availability (visual estimates of percent cover for each understory species), forage use (evidence of browsing), diet and animal condition (pellet group collections), snow depths (four measurements at each corner of the plot), distance to openings or cover, and animal activity associated with the site. Forage availability and snow depths were also measured in the permanent plots. At least five plots in each habitat type were assessed during intensive monitoring periods. If snow conditions remained unchanged, other plots in each habitat type were visited until conditions dictated the end of an intensive monitoring period.

To assess elk preference or selection for specific site characteristics, habitat use data were compared with data collected from the permanent plots.

3.2.5 Habitat selection analyses

Various indices were used and compared to assess not only habitat selection, but the relative merits of each method employed. Seasonal habitat preferences were determined using three indices: Strauss' linear model (1979), a derivation of the chi-squared approach (Neu *et al.* 1974), and a modification of habitat use in proportion to habitat availabilities.

In addition, winter habitat use was assessed by comparing relative proportions of different habitat components within a home range with home range sizes. Proportions of forage classes and individual forage species were also compared to home range sizes to determine if relationships existed between home range size and forage availability. Proportions of forage species were determined from visual estimates of species coverage in permanent plots on the winter range and temporary plots on summer ranges.

Seasonal forage preferences were assessed from rank comparisons of usage and availability.

Relationships between certain habitat variables (percent cover by species and forage classes [below 2 m] and canopy closure) and habitat use (locations per hectare) were evaluated using linear regression and multiple regression techniques. Normality tests of the data were conducted to determine whether parametric or non-parametric analogs should be used for analyses.

3.2.6 Animal activity monitoring

Elk activity was recorded with a Rustrak recorder (Gulton Industries Inc., Manchester, New Hampshire) and a Telonics receiver/digital processor from tip-switch radio-collared elk during most winter intensive monitoring sessions, 24 hours a day. During the first two sessions in 1983, activity was not monitored because of receiver failure. Activity strip charts were divided into 0.1-hour intervals and analysed manually for inactive and active signals based on amplitude and pulse rate information.

Simultaneous observation-activity recording done on captive elk at the Vancouver Game Farm, Cloverdale, B.C., showed that active recorded signals were indicative of active behaviours (grazing, browsing, standing, and travelling), and inactive recorded signals were indicative of inactive behaviours (bedding, ruminating, and standing). Gillingham and Bunnell (1984), studying activity of black-tailed deer, found that tip-switch collars recorded active:inactive ratios correctly (compared to observed activity) 90% of the time.

3.3 Weather Monitoring

Two CR-21 weather stations (Campbell Scientific Ltd., Edmonton, Alberta) were used to monitor temperature, wind speed, and wind direction continuously at different periods throughout the study. From November through March (1982/83, 1983/84, and 1984/85), these stations were placed in open sites at the southern and northern ends of the Greenstone herd winter range (Loveland Bay and Cranberry Hill, respectively). In the summer (May through September) of 1983, one station was placed in an open 15-year-old second-growth stand and one in an adjacent old-growth stand on the Grilse herd summer range to compare temperature and wind speeds. In the 1984 summer, both stations were located in the open; one on the low-elevation (400 m) range of a resident herd and the other on the higher elevation (750 m) summer range of the Grilse herd. A Stephenson Screen monitoring device was placed in an open site near Swamp Lake (Grilse herd's winter range) from June 1981 through April 1982.

Daily maximum, minimum and mean temperatures were recorded at all weather stations and averaged for stations at similar elevations to obtain monthly mean values. Temperature data from the Swamp Lake station for April through October 1981, and mean values from the Swamp Lake and Loveland Bay station for November through March (1981 through 1986), were compared with values collected by Air Studies Branch near Merrill Lake (Greenstone herd's winter range) for the 11-year period before the study (1970 through 1980).

During the winters of 1982/83, 1983/84, and 1984/85, snow depths were periodically measured in the open at permanently staked road locations. At each location, four measurements were taken and averaged.

A winter severity index (Janz 1983) was computed based on annual snow depth profiles from Janz (1983) and this study, by dividing the area under each snow depth curve by the area under the curve for the winter of 1977.

3.4 Diet Composition and Quality Analyses

Fresh fecal samples were collected from groups of elk containing radio-collared individuals from each of the two main herds under study (Grilse and Greenstone) at least monthly from March 1981 through March 1985. About 10-20 pellets were collected from at least eight fresh pellet groups to compose a single sample used in fecal nitrogen (N) and diet analyses. An initial pilot study to estimate the coefficient of variation of fecal N between pellet groups composing a sample was conducted on 22 samples. Coefficients of variation averaged around 7%, suggesting that a confidence level of around 95% could be obtained with this level of sampling by combining pellet collections from groups of elk on a particular collection day. Composite fecal samples from several collection days were grouped to estimate seasonal diets on a herd area basis, except during the winter of 1984/85 when diet was estimated from each collection date.

Seasons were delineated according to the following dates: spring - April 1 - June 14; summer - June 15 - September 14; fall - September 15 - November 14; early winter - November 15 - January 31; late winter - February 1 - March 31.

Three sets of paired rumen and fecal samples were obtained from hunter-killed elk taken in October and November 1981. Hunters were requested by letter to collect several handfuls of rumen material and one to two handfuls of fresh fecal material from the lower portion of the large intestine. The samples were analysed for forage species content to compare results from these two methods of determining food habits.

Diet composition was estimated for 53 samples collected from all herds and seasons by fecal fragment analysis (Sparks and Malechek 1968; Ward 1970; Davitt and Nelson 1980). Forage voucher slides of approximately 50 species, collected and prepared for a previous study on Vancouver Island (Janz 1983), were used to identify epidermal fragments. Percent species composition of diets was determined from eight slides of fecal material and 300 fields of view for each diet.

A griddled eyepiece was used to estimate the percent of area covered by each species in each field of view. Percent coverages were totalled to calculate percent of diet by species. All diet sample analyses were done by the Wildlife Habitat Laboratory, Washington State University, Pullman, Washington.

Percent fecal N or fecal crude protein (% fecal N x 6.25) was used as an indirect index of diet quality. Significant correlations between fecal crude protein and measures of diet quality have been reported for bighorn sheep (Hebert 1973) and Roosevelt elk (Janz 1983). Fecal samples were analysed for fecal N by the Wildlife Habitat Laboratory, Washington State University. Dietary protein levels were estimated from fecal crude protein values with the regression developed by Janz (1983):

$$Y = 0.71X$$

where Y is dietary crude protein, and X is fecal crude protein.

Diaminopimellic acid (DAPA), an indigestible by-product of rumen fermentation, was used as an indicator of digestible energy (DE) levels in diets. Nelson *et al.* (1982) found in controlled studies that DAPA levels in fecal samples were directly related to digestible energy of the diet. Diet DE levels were estimated from DAPA levels from the regression (B. Davitt, Wash. State Univ., pers. comm., April 1987):

$$Y = 30.328 + 29.424X$$

where Y = %DE, and X = DAPA in mg/g fecal dry matter. The regression was developed in feeding trials using mule deer (*Odocoileus hemionus*), where a significant relationship (r = .95) between diet DE and fecal DAPA was noted. The relationship between fecal DAPA and diet DE levels for elk are currently unavailable. Dry matter digestibility (DMD) of elk diets was estimated from estimated DE using the relationship (Mould and Robbins 1982):

$$Y = -0.61 + 0.98X$$

where Y = DE, and X = DMD; $r^2 = .98$.

Twenty-five forage species collected during January and February of 1984 were analysed for tannin content (mg/g) by the Ministry of Environment, Environmental Soils Laboratory, Kelowna, B.C. Quantitative techniques from Hagerman and Butler (1978) were followed in the assessments.

3.4.1 Diet selection analyses

Estimates of species availability on seasonal ranges were calculated by combining species cover values (visually estimated) in each stand type (summer range) and habitat type (winter range). These values were adjusted by the relative proportion of the seasonal range that each type represented. Linear and Spearman rank correlation analyses were used to compare availability and use of dietary items. Selection was considered to be related not only to preference for a forage item, but also to the availability or inaccessibility of a food item.

Diet selection was analysed by several techniques. Ranks of usage and availability (Johnson 1980) were used only for the summer diets because of a correlation between use and availability. Johnson's ranking technique, however, is biased because of unequal abundances. Therefore, for winter diets, where bias was evident, various indices of preference were compared and Strauss' (1979) linear index was used.

3.5 Animal Condition Assessments

3.5.1 Fecal sample analyses

Percent fecal N or fecal crude protein (% fecal N x 6.25), and diaminopimellic acid (DAPA) levels of fecal samples collected from free-ranging elk were used as a general index of animal condition for herds in the study area. Approximately 200 samples collected from all herds and seasons throughout the study area were analysed for percent fecal N levels. DAPA levels from samples grouped by season were estimated for all herds in the study area for the period May 1981 - March 1982. All fecal sample analyses were conducted by the Wildlife Habitat Laboratory, Washington State University, Pullman, Washington.

3.5.2 Kidney fat index analysis

The kidney fat index (KFI) was calculated for 67 hunter-collected samples obtained during the fall in 1981 through 1985 using the formula (Riney 1955):

$$KFI = \frac{\text{perinephric fat weight}}{\text{kidney weight}} \times 100$$

A significant relationship between KFI and total body fat has been demonstrated in East African ungulates (Smith 1970), and Riney's method has been used extensively as an indicator of plane of nutrition (Hanks 1981).

3.6 Population Assessments

3.6.1 Aerial survey techniques

Helicopter surveys, using a Bell 206 Jet Ranger, were conducted at least twice annually from 1982 to 1985. August surveys were conducted to estimate calf:cow ratios that would serve as an index of productivity; April-May surveys were conducted to estimate calf:cow ratios to serve as an index of recruitment. Sample sizes were derived using the formula (Cochran 1977):

$$n = \frac{(N_0)}{1+(N_0/N)}$$

where: $N_0 = t^2 \left(\frac{pq}{d^2}\right)$

N = estimated herd size
n = sample size required
t = the t-value for the appropriate confidence interval
p = the calf:100 cow ratio
q = 1-p
d = the maximum desired error (3%) in the calf:100 cow ratio

Population estimates were made based on composite information from Petersen index calculations (Seber 1973) and on general knowledge of the herds from extensive aerial surveys conducted during 1981 and 1982.

Yearling female calves (older than 12 months of age) were generally indistinguishable from adult cows during aerial surveys and were included as cows in all estimates of calf:cow ratios. A correction factor for yearling female calves was incorporated only when survival rates were estimated. Calf survival was estimated using the difference in calf:cow ratios between August surveys and April surveys of the following year. These indices were adjusted for estimated cow mortality over the same period.

3.6.2 Fecundity assessments

Female reproductive tract samples were collected from cow elk harvested in the study area during the fall hunting seasons of 1981 through 1985. Samples were examined for the presence of a fetus. Samples collected before November were not included in the analyses because earlier pregnancies may not have been detectable with normal macroscopic methods. Fetus size (crown to rump length) was used to estimate conception and parturition dates (Trainer 1971). Samples from other areas were combined with samples from the study area to estimate both overall pregnancy rates and age-specific pregnancy rates for Vancouver Island cow elk.

3.6.3 Life table analyses

Life tables were constructed for the female segment of the population using age structure data collected from elk harvested in the study area from 1981 to 1984, inclusive, and from radio-collared elk. Age structure data from adjacent areas (including the Adam, White, Gold, Muchalat, Ucona, and Heber River watersheds) were included with data from the study area to construct comparative life tables (Figure 2).

Life tables were calculated using the procedure as outlined by Caughley (1977). Data were exponentially transformed and smoothed by the log-polynomial form of the quadratic equation. Smoothing the data was required to reduce sampling variation and bias. All four schedules of the life table were calculated: l_x (survivorship), d_x (mortality), q_x (mortality rate), and p_x (survival rate).

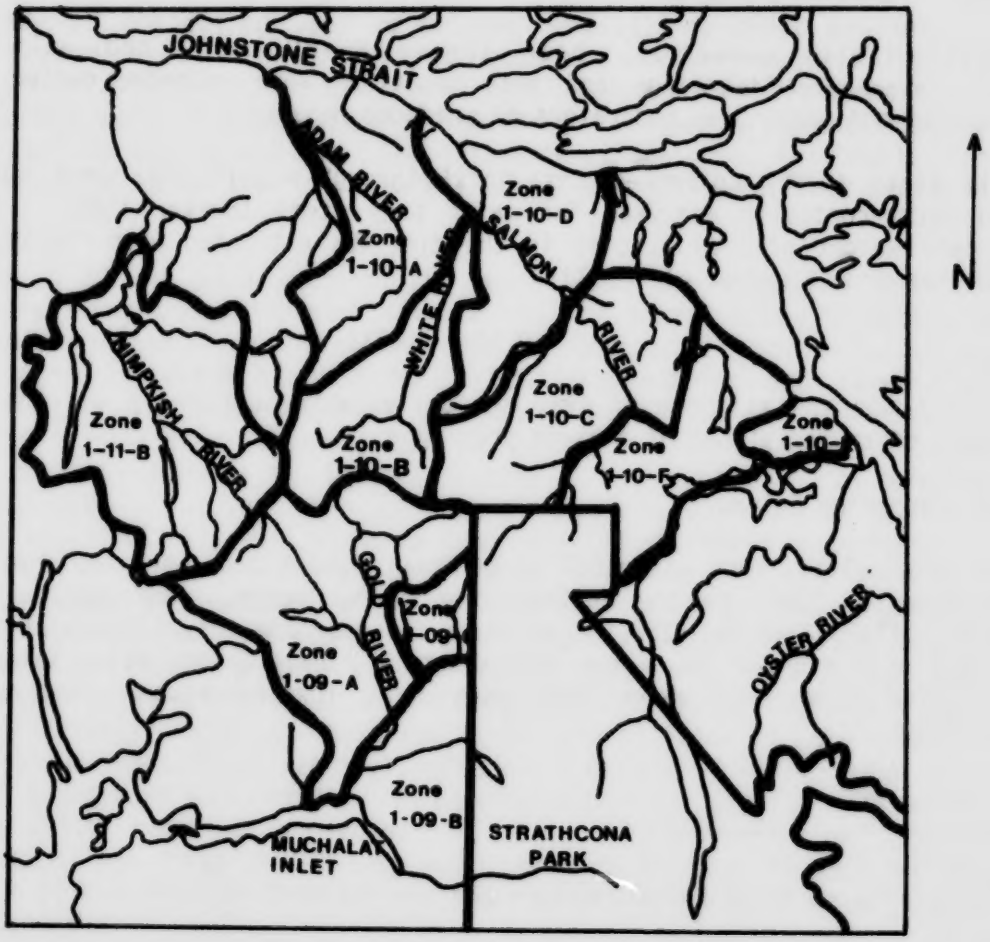


Figure 2. Locations of Management Unit zones in the study area where age structure data were collected to construct life tables (1-10-C, 1-10-D, 1-10-E, and 1-10-F). Comparative life tables were constructed with additional data from the Adam (1-09-A), White (1-10-B), Muchalat and Gold (1-09-A), Ucona (1-09-B), and Heber River (1-09-C) watersheds.

In addition, life tables were calculated for the male segment of the population. However, males had a highly biased age structure because of harvesting restrictions and hunter bias for larger animals, so these tables were used only for illustrative purposes.

3.6.4 Predation analyses

Cougar (*Felis concolor*), bear (*Ursus americanus*), and wolf (*Canis lupus crassodon*) sightings and scat locations were recorded during regular road use and applied as indicators of predator density.

Wolf scats (n=95) collected from April through August 1981 were autoclaved and microscopically analysed for major prey items (Becker 1982). Relative percent weight of prey species in the diet was estimated with the regression equation from Floyd *et al.* (1978):

$$Y = 0.38 + 0.02X;$$

where Y was the kilogram of prey per collectable scat and X was the average weight of an individual of a given prey type.

3.7 Capturing Calves

Two male calves, each estimated to be about 1 week old, were captured by hand on June 10, 1982, on the Grilse Creek summer range. One was the calf of radio-collared cow No. 252. They were fed approximately 170-230 mL of whole goat's milk every 2 hours for approximately 2 days before being taken to the Vancouver Game Farm where they were kept for subsequent captive animal studies.

4.0 RESULTS AND DISCUSSION

4.1 Study Animals

4.1.1 Immobilization data

The accuracy of the method used to deliver immobilizing drugs was severely reduced beyond about 20 m. Three complete misses occurred during immobilizations attempts. One elk was struck, apparently in the abdomen, but was not located again despite extensive searching. One mortality occurred when an adult cow elk, darted and under the influence of the drug, ran into a stand of spacing debris up to 1 m in depth where she apparently fell and broke her neck.

The remaining 33 elk were successfully immobilized and located. Induction and recovery times using fentanyl citrate did not appear to be dependent on dosage (which ranged from 78 to 108 mg) or whether or not xylazine was included in the solution administered. Induction and recovery times along with vital signs of immobilized elk are summarized in Table 3. Recommended dosages for immobilizing Roosevelt elk on Vancouver Island are 90-105 mg of fentanyl in combination with 50 mg xylazine. Higher dosages of xylazine appeared to make elk quite unsteady during recovery. Sixteen to 20 mg of diprenorphine was usually sufficient to produce a smooth, rapid recovery.

Most elk responded predictably, with induction and recovery times of about 10 minutes using fentanyl citrate and the antagonist diprenorphine injected intramuscularly. However, some very different reactions, such as extremely long induction or recovery times or only partial immobilizations, were noted for several animals. Most of these reactions were believed to be a result of using either an unbuffered fentanyl solution more than 1 or 2 weeks after mixing, or a buffered solution kept in unrefrigerated storage for many months. One elk, which required a second injection of fentanyl for complete immobilization, was first darted very near the anus and it was suspected that some or all of the drug may have entered the rectum where incomplete absorption may have occurred.

It is recommended that fentanyl in a powdered form be dissolved in a buffered, distilled water solution of pH 3.5 to 4.0 and kept refrigerated during storage in a dark bottle. Freezing causes an insoluble precipitate to form, and the solution is more stable under dark conditions. It appears that 30 mg/mL is the maximum concentration to which powdered fentanyl can be mixed. Buffered fentanyl solutions stored at room temperature for extensive periods may not produce the smooth, quick inductions noted with recently mixed solutions. One mixture, which had been stored at room temperature, effectively immobilized elk 13 months after being prepared, but 30 months after preparation crystals had formed so that the mixture was no longer usable.

Table 3. Information obtained from elk immobilized with fentanyl citrate

Animal Ident.	Collaring Date	Sex	Age (yr.)	Dosage (mg)			Induction (min)	Recovery (min)	Resp. rate (/min)	Heart rate (/min)	Rectal temp.(°C)	Comments
				Fentanyl citrate	Xylazine	Diprenorphine						
61	Mar/81	F	2.8	90	--	16	12	6	24	56	--	periodic muscle tensing
262	Mar/81	F	3.8	90	--	16	9	10-15	20	56	40.0	periodic muscle tensing
371	Mar/81	M	2.8	90	--	16	unknown	12	--	--	41.3	panting during reversal
1063	Mar/81	F	9 mos	90	--	14	12	4	16	64	--	muscle tremors
291	Mar/81	M	2.8	90	--	16	7	6	20	56	39.5	periodic tensing
81	Mar/81	F	9 mos	90	--	14	11	7	--	--	--	
1014	Mar/81	F	10.8	90	--	16	10	5	10	52	40.6	
332	Mar/81	F	3.8	90	--	12	9	N11 @ 10	20	60	40.8	muscle tensing and rigidity
						4		13				
432	Mar/81	F	6.8	90			--					unbuffered fentanyl solution
				90	--	32	12	6	62	68	42.2+	1 week old used
241	Mar/81	M	1.8	90	100	15	6	N11 @ 26	12-24	56	40.6	bedded near capture site
						12		30				following reversal
22	Mar/81	F	3.8	90	100	15	10	22	12	52	40.0	
410	Mar/81	M	1.8	90	100	12	11	15	20	48	39.3	slow recovery
42	Mar/81	F	8.8	90	100	15	12	7	14	52	39.2	muscle rigidity
311	Mar/81	F	3.8	90	100	15						
				90	100	15	12	22	12-16	42-52		slow recovery
					(50 min later)	(14 min later)						
1037	Mar/81	F	14.8	90	20	16	13	10	6	44	39.1	
252	Mar/81	F	14.8	90	20	16	unknown	7	6	40	40.6	

Table 3. (Continued)

Animal Ident.	Collaring Date	Sex	Age (yr.)	Dosage (mg) Fentanyl citrate	Xylazine	Diprenorphine	Induction (min)	Recovery (min)	Resp. rate (/min)	Heart rate (/min)	Rectal temp.(°C)	Comments
271	Apr/81	F	3.9	108	20	16	9	6	12	60	40.6	
342	Apr/81	F	6.9	108	20	16	18	6	8	52	39.6	
1140	Apr/81	M	10.9	90	40	56	unknown	66	10	88	41.5	extremely slow recovery unstable drug suspected
490	Feb/82	F	2.7	105	100	20	9	9	12	36	37.5	no tensing or muscle tremors
631	Mar/82	F	12.8	105	50	20	10	10	8	44	38.7	thrashed when head position changed
621	Mar/82	M	2.8	105	50	20	5	--	6-8	62-102	38.1	periodic tensing
						6 (30 min later)		42				
611	Mar/82	M	2.8	90	100	24	unknown	12	18	60	37.3	very heavily sedated 60 min after darting
591	Mar/82	F	14.8	90	100	24	--	--	6	40	40.2	drug from first dart may have been injected into rectum
				90	100 (73 min later)	8 (27 min later)	10	28				
641	Mar/82	F	8.8	90	100	16	9	18	16	84-88	39.8	periodic tensing & leg thrashing; unsteady recovery
561	Apr/82	F	12.9	90	100	16	unknown	13	15	46	38.5	periodic tensing & leg thrashing
540	Nov/82	F	3.6	105	100	20	6	8	11-14	36-48	--	continuous salivation; periodic thrashing when head position changed
1281	July/83	F	12.0	78	50	20	6	5	28	56	--	45 minutes before complete immobilization occurred
1085	Mar/84	F	3.8	90	50	20	8	12	10	--	--	very deeply sedated
601	Sept/84	F	5.5	90	50	18	22	5	32	40-50	--	sensitive to handling
551	Sept/84	F	4.5	105	50	18	29	8	16	42	--	

4.1.2 Ages, body measures, and blood analyses

Ages, body measures, and estimated weights of immobilized female and male elk are presented in Tables 4 and 5, respectively. Mean shoulder height, and chest girth of calf and 2-year-old immobilized elk were greater than those reported by Blood and Smith (1984). Small sample sizes, slight differences in measurement techniques, and differences in animal age at the time of measurement may explain these differences. Mean body measurements of immobilized adult female elk were very similar to those noted by Blood and Smith (1984).

Blood serum parameters obtained from SMA-12 and progesterone level analyses of serum samples are summarized in Table 6. Karns and Crichton (1978) and Wesson *et al.* (1979) found that most blood variables were not affected by capture and handling in caribou (*Rangifer tarandus*) and white-tailed deer (*Odocoileus virginianus*).

Most serum constituent levels of immobilized elk were within the range of values reported for elk as reviewed by Weber (1981). Albumin levels, which have been shown to reflect range quality (Weber *et al.* 1984), were mostly near the upper end of the normal range reported, suggesting that the immobilized elk were on a relatively high nutritional plane. However, this is confounded by urea nitrogen levels that were mostly lower than the lowest values previously recorded for elk. The ability of urea nitrogen levels to reflect animal condition is probably not as reliable as albumin levels since other factors can also affect the assay results. Both calcium and phosphorus levels were at the upper end of the normal range of values reported by Weber (1981).

Weber *et al.* (1984) recorded serum progesterone levels for Rocky Mountain elk (*Cervus elaphus nelsoni*) whose pregnancy status was also confirmed through rectal palpation. The lowest value recorded for a pregnant elk was 3.7 ng/mL, while the highest level from a non-pregnant individual was 1.3 ng/mL. The lowest value recorded from four adult female elk tested (aged 2 years 8 months, 9, 13, and 15 years) was 5.0 ng/mL, suggesting all were pregnant.

Of the 21 radio-collars placed on elk in 1981, at least two were functioning on live elk in May 1986, and two others were transmitting: one from a radio-collar that had worn out and dropped off the animal, and another from the site where an elk had died during the winter of 1985/86. Most collars appeared to be functioning well for at least 4 years after being installed. The known status of radio-collared elk as of May 1986 is summarized in Table 7.

Two of five radio-collars fitted on male elk, which used seat belt retractor components to allow for neck expansion, were dropped within 7 months of being

Table 4. Body measurements and estimated weights of immobilized female elk

Animal identifier	Age (yr)	Total length (cm)	Hind foot length (cm)	Shoulder height (cm)	Chest Height (cm)	Chest girth (cm)	Estimated[1] weight (kg)
1063	9 mos	186	63.5	136	71	140	181.6
81	9 mos	197	65	140	72	144	193.8
Mean female calves		191.5	64.3	138	71.5	142	187.7
222	2.7	---	63	142	75	152	218.3
61	2.8	201	65	148.5	71	176	291.8
490	2.7	---	63	148	--	152	218.3
Mean female 2-year-olds		201	63.7	146.2	73	160	242.8
391	3.7	---	65	145	88	160	242.8
262	3.8	215	66	140	71	172	279.5
332	3.8	---	68	143	74	168	267.3
22	3.8	252	64	150	74	172	279.5
311	3.8	220	65	149	83	158	236.7
271	3.9	228	64	151	87	168	267.3
540	3.6	217	62.5	151	76.5	168	267.3
1085	3.8	---	--	---	--	168	267.3
342	6.9	228	65	157	85	184	316.2
432	6.8	209	64.5	145	72	158	236.7
Capture Mortality	8.8	211	64	156	77	168	267.3
641	8.8	226	64	149	85	158	236.7
42	8.8	229	66	150	83	170	273.4
1014	10.8	236	--	---	--	164	255.0
631	12.0	232	63.5	151	82.5	160	242.8
561	12.9	241	63	149	86	164	255.0
252	14.8	234	63	157	84	168	267.3
1037	14.8	231.5	66	155	83	170	273.4
591	14.8	221	65	146	82	164	255.0
1281	12.0	---	--	---	--	---	---
601	5.5	---	--	---	--	172	279.5
551	4.5	---	--	---	--	168	267.3
Mean female adults		226.9	64.6	149.6	80.8	166.8	263.5

[1]From the regression Y = 3.06X - 246.8 (where Y = wt in kg; X = chest girth in cm; r = .91) developed from a sample of 21 yearling and older female Roosevelt elk collected on Vancouver Island. Data on file - B.C. Ministry of Environment, Nanaimo, B.C.

Table 5. Body measures and estimated weights of immobilized male elk

Animal identifier	Age (yr)	Total length (cm)	Hind foot length (cm)	Shoulder height (cm)	Chest Height (cm)	Chest girth (cm)	Estimated[1] weight (kg)
241	1.8	210	66.5	144	81	150	212.2
410	1.8	232	67	145.5	84	156	230.6
Mean male yearlings		221	66.8	144.8	82.5	153	221.4
291	2.8	230	71.5	147	70	166	261.2
371	2.8	230	71.5	173	65	180	304.0
611	2.8	239	--	---	--	152	218.3
621	2.8	244	72	162	91	164	255.0
Mean male 2-year-olds		235.8	71.7	160.7	75.3	165.5	259.6
1140	10.9	235	--	162.5	80	184	316.2

[1]From the regression Y = 3.06X - 246.8 (where Y = wt in kg; X = chest girth in cm; r = .91) developed from a sample of 21 yearling and older female Roosevelt elk collected on Vancouver Island. Data on file - B.C. Ministry of Environment, Nanaimo, B.C.

Table 6. Blood serum parameters of 22 immobilized elk

Animal identifier	Sex	Age (yr)	Capture date	Total Protein g/dL	Calcium mg/dL	Phosphorous mg/dL	Albumin g/dL	Globulin g/dL	Glucose mg/dL	Urea nitrogen mg/dL	Uric acid mg/dL	Bilirubin (total) mg/dL	Alkaline phosphatase IU	LDH IU	SGOT IU	Progesterone ng/mL
1003	F	9 mos	Mar. 13/81	6.4	9.5	6.2	3.5	2.9	111	15	0.6	0.2	114	379	30	—
400[a]	F	2.7	Feb. 3/82	6.4	8.8	5.5	3.0	—	67.5	14	0.2	0.2	496	446	83	5.5
311	F	3.8	Mar. 5/81	6.0	9.6	4.5	3.5	2.5	124	9	0.7	0.2	154	282	33	—
22	F	3.8	Mar. 10/81	5.7	9.1	5.4	3.3	2.4	123	8	1.0	0.3	175	232	27	—
332	F	3.8	Mar. 12/81	6.2	9.6	6.5	3.9	2.3	129	8	0.7	0.4	144	273	33	—
262	F	3.8	Mar. 24/81	6.2	8.9	7.6	3.1	3.1	80	12	0.5	0.6	131	292	47	—
271	F	3.3	Apr. 1/81	6.9	8.8	6.3	2.3	4.6	108	10	0.8	0.2	34	262	35	—
342[a]	F	6.9	Apr. 1/81	6.9	9.2	4.7	3.5	3.4	55	19	0.5	0.2	77	287	35	—
432	F	6.8	Mar. 25/81	6.3	9.5	6.0	3.5	2.8	78	12	0.7	0.2	85	375	30	—
Capture Mortality	F	8.8	Mar. 24/81	8.1	11.3	10.5	4.0	4.1	10	15	1.1	0.2	168	855	171	—
42	F	8.8	Mar. 10/81	5.7	8.5	5.4	3.3	2.4	148	11	0.7	0.2	138	292	32	—
641[a]	F	8.8	Mar. 31/81	6.2	8.9	4.4	2.9	—	96	9	0.2	0.2	69	269	68	5
861[a]	F	12.8	Apr. 7/82	6.0	8.6	5.0	2.6	—	102	9	0.1	0.2	400	341	88	8.3
252[a]	F	14.8	Mar. 30/81	6.4	9.0	5.7	3.7	2.8	79	16	0.6	0.2	70	326	30	—
1037[a]	F	14.8	Mar. 30/81	6.3	8.8	6.4	3.7	2.6	76	28	0.7	0.2	19	303	28	—
981[a]	F	14.8	Mar. 31/82	6.8	8.8	4.2	2.9	—	106	23	0.2	0.4	306	325	86	7.5
410	M	1.8	Mar. 10/81	5.8	10.1	8.2	3.4	2.4	148	10	0.8	0.2	99	348	48	—
241	M	1.8	Mar. 11/81	5.5	9.1	8.4	3.0	2.5	159	5	0.7	0.2	54	350	48	—
291	M	2.8	Mar. 13/81	6.8	8.4	5.4	3.2	3.6	82	14	0.5	0.3	29	383	48	—
621	M	2.8	Mar. 16/82	5.9	10.0	4.5	2.8	—	129	10	0.2	0.3	203	449	90	—
611	M	2.8	Mar. 18/82	6.5	9.4	8.4	2.8	—	107	12	0.4	0.3	212	367	105	—
1140	M	10.8	Apr. 9/81	5.9	9.0	2.9	3.0	2.9	78	22	1.1	0.2	209	404	56	—

[a]Duplicate samples run; values presented are means of runs.

Table 7. Known status of radio-collared elk as of May 1986

Animal identifier	Sex	Herd	Capture Date	Date of death, collar drop, or disappearance	Age at death (yrs)	Cause of Death	Length of time radio-collared
Mortalities							
81	F	L. Salmon	Mar/81	May/81	1	Poached	2 mos
22	F	Grilse	Mar/81	June/81	4	Wolf kill[1]	3 mos
1063	F	L. Salmon	Mar/81	Summer/82	2	Natural[1]	approx. 18 mos
342	F	L. Salmon	Apr/81	Nov/82	8.6	Wounded, then wolf killed	20 mos
332	F	White River	Mar/81	Dec/83	6.6	Legal kill	33 mos
1281	F	Greenstone or Swamp Lake	July/83	Jan/85	13.7	Poached	17 mos
262	F	Greenstone	Mar/81	Feb/86	8.7	Poached	59 mos
252	F	Grilse	Mar/81	Approx. Mar/86	19.8	Natural[1]	60 mos
241	M	Grilse or Greenstone	Mar/81	Aug/81	2.2	Natural[1]	5 mos
410	M	Grilse	Mar/81	Aug/81	2.2	Natural	5 mos
611	M	Greenstone	Mar/82	Fall/82	3.5	Poached[1]	approx. 7 mos
Dropped collars							
371	M	Grilse	Mar/81	July/81	---	---	4 mos
1140	M	Greenstone	Apr/81	Oct/81	---	---	7 mos
291	M	L. Salmon	Mar/81	1983	---	---	approx. 24 mos
391	F	Grilse	Feb/81	1985	---	---	approx. 48 mos
Disappearances							
311	F	Greenstone	Mar/81	Oct/81	---	---	7 mos
621	M	Grilse	Mar/82	May/83	---	---	14 mos
Functioning collars on live elk							
1014	F	Grilse	Mar/81	---	---	---	62 mos
271	F	Grilse	Apr/81	---	---	---	61 mos
631	F	Grilse	Mar/82	---	---	---	50 mos
641	F	Greenstone	Mar/82	---	---	---	50 mos
1085	F	Grilse	Mar/84	---	---	---	26 mos
551	F	Greenstone	Sept/84	---	---	---	20 mos
601	F	Greenstone	Sept/84	---	---	---	20 mos
540	F	Swamp Lake	Nov/82	---	---	---	42 mos
Other							
61	F	Greybe's	Mar/81	Jan/86-Transplanted; antenna broken but transmitting			58 mos
1037	F	Grilse	Mar/81	Aug/85 - Observed; collar not transmitting			53 mos

[1]Assumed from observation and available information

installed. Two other seat belt-modified collared males died 5 months after radio-collaring, while the other male dropped his collar about 2 years after being radio-collared. Expandable collars malfunctioned after being in place as little as 5 months, suggesting that the seat belt retractor modification system is not an adequate method of allowing for neck expansion in radio-collared bull elk. The surgical tubing modification system appeared more functional. Only one collared female dropped a radio-collar, apparently from rubbing against a tree about 4 years after radio-collaring.

4.2 Weather

4.2.1 General climatic conditions

Mean monthly temperatures in winter were slightly higher during the study than during the previous 11-year period (1970-1980), while spring and summer temperatures were slightly cooler during the study. In all instances, however, temperatures were comparable to average values collected during the decade before the study (Figure 3).

R. Page (B.C. Ministry of Forests, pers. comm., Feb.1987) analysed winter snow depth trends on Vancouver Island from the late 1890's until present and noted that extreme winter snowfalls occur at regular 18-year intervals, with a cyclical trend in winter severity occurring in the intervening years. The end of this study coincided with the end of a decade of mild winters and from historical patterns it appears that winter severity will increase in the coming decade. Winter severity is a major factor influencing population performance of large ungulates (Jones and Mason 1983; Mech *et al.* 1987) and the availability of adequate winter ranges to satisfy elk requirements on Vancouver Island will likely be more critical during the coming decade than in the last.

4.2.2 Winter snow patterns

4.2.2.1 Snow accumulation patterns

Snow accumulations were monitored throughout the winter of 1984/85 at five permanent monitoring stations located in open sites at various elevations on the winter range. Although snow accumulations were often greater than 20 cm in depth, the duration of the snowpack was limited. Melt periods occurred where virtually all of the snow disappeared at low elevations. Habitat use and diet composition differed between this winter and mild winters (Section 4.7.4.1).

Monitoring sessions were initiated whenever a significant snow event occurred (Section 3.2.4). The mean depths at each snow station during the intensive monitoring sessions and the fluctuations of snow accumulations throughout the winter are presented in Table 8 and Figure 4, respectively. The Morton Road

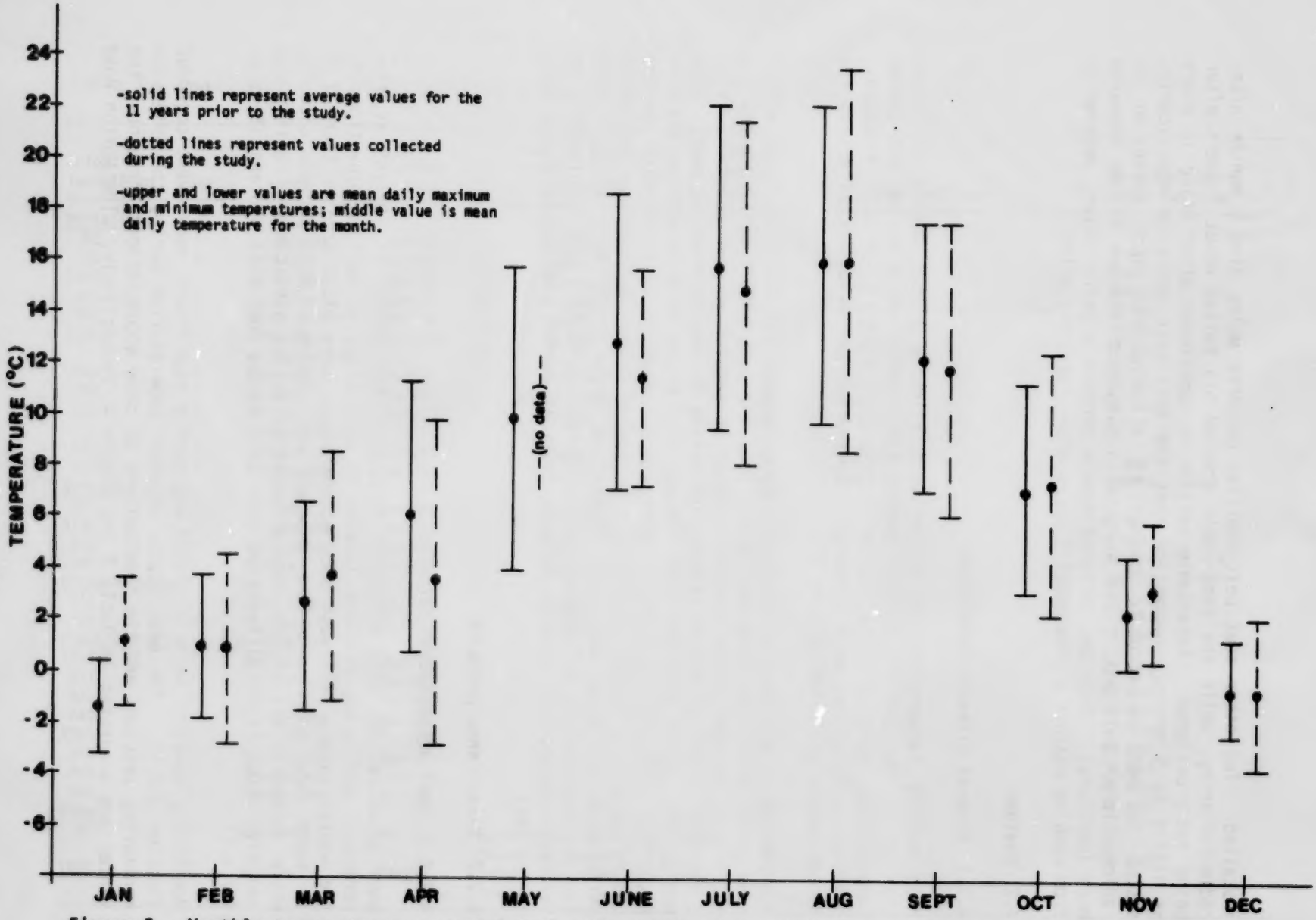


Figure 3. Monthly temperatures recorded during the study (1981-1986) and during the previous 11 years (1970-1980).

Table 8. Permanent snow station data for the 1984/85 winter (mean snow accumulation by monitoring sessions)

Station	Monitoring sessions	Date	n	Mean	SD
Mohun Gravel Pit	One	Nov. 27-Dec. 6	9	10.389	2.21
Cranberry Junction	One	Nov. 27-Dec. 6	6	19.958	3.14
Morton Road	One	Nov. 27-Dec. 6	6	30.458	4.96
Gosling Junction	One	Nov. 27-Dec. 6	6	24.583	2.45
Loveland Bay	One	Nov. 27-Dec. 6	6	20.833	4.02
Mohun Gravel Pit	Two	Dec. 30-Jan. 3	2	20.87	.53
Cranberry Junction	Two	Dec. 30-Jan. 3	2	17.625	6.19
Morton Road	Two	Dec. 30-Jan. 3	4	32.50	6.64
Gosling Junction	Two	Dec. 30-Jan. 3	2	29.75	2.12
Loveland Bay	Two	Dec. 30-Jan. 3	1	24.00	0
Mohun Gravel Pit	Three	Feb. 5-Feb. 13	8	12.28	5.76
Cranberry Junction	Three	Feb. 5-Feb. 13	6	18.92	8.34
Morton Road	Three	Feb. 5-Feb. 13	8	45.19	8.84
Gosling Junction	Three	Feb. 5-Feb. 13	5	33.40	8.29
Loveland Bay	Three	Feb. 5-Feb. 13	4	17.25	5.68
Mohun Gravel Pit	Four	Feb. 19-Feb. 28	0	0	0
Cranberry Junction	Four	Feb. 19-Feb. 28	2	6.75	9.55
Morton Road	Four	Feb. 19-Feb. 28	3	40.5	4.63
Gosling Junction	Four	Feb. 19-Feb. 28	2	21.75	2.47
Loveland Bay	Four	Feb. 19-Feb. 28	3	16.83	5.62

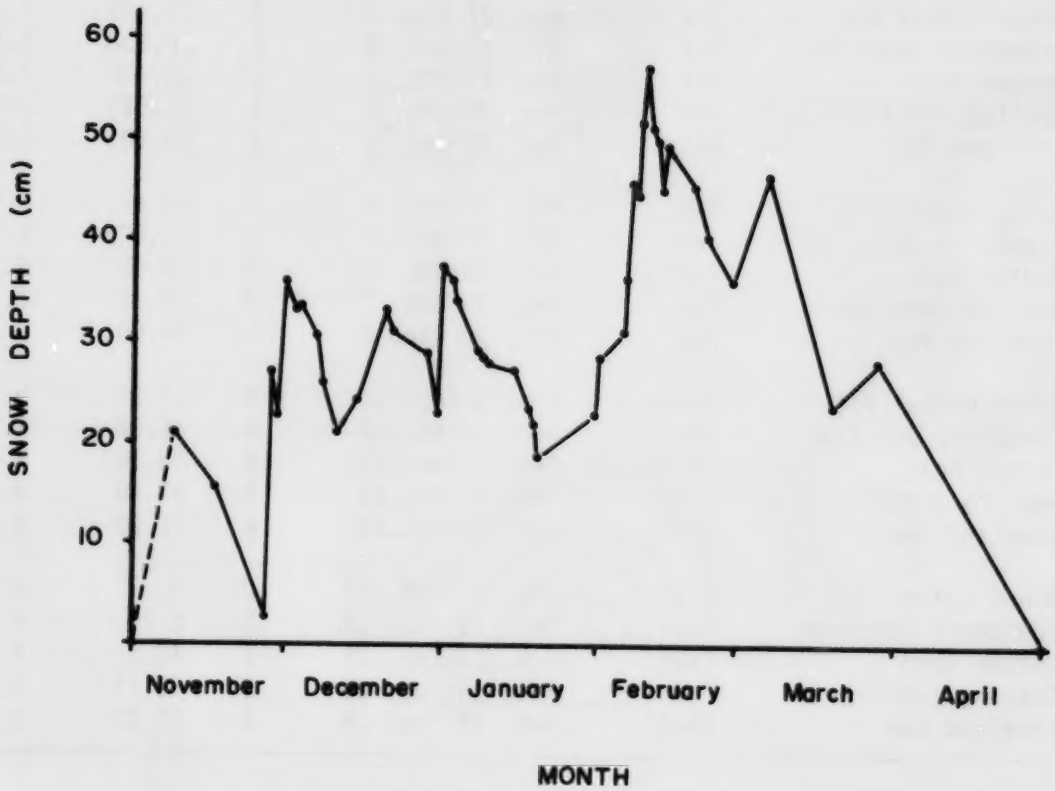


Figure 4. Snow depth fluctuations throughout the moderate winter of 1984/85 (Mohun Lake Road station).

station (at an elevation of 200 m) was consistently monitored over the winter to assess snow trend patterns during and outside monitoring periods. These data were also used for comparison with other years in calculating the winter severity index (Section 4.2.2.2). Because this site was higher in elevation than most of the other snow stations, shaded by surrounding large trees, and flat (no slope to aid in water run-off), snow accumulations tended to last longer at this site than over the rest of the winter range. Monthly snow depths are also listed to show the snow patterns over the entire winter (Table 9). Mean monthly snow depths for each station were lower than monitoring session depths because melt measurements were also included.

Snow accumulations (using Morton Road station) differed between some monitoring sessions. During monitoring session one, snow depths did not significantly differ from monitoring session two, but did differ from sessions three and four ($.01<p<.025$). Snow depths in monitoring session two differed from monitoring session three ($.025<p<.05$), but not session four. Snow depths in monitoring sessions three and four did not significantly differ ($.05<p$).

All snow station accumulations significantly differed during the moderate winter ($p<.0005$) even though some stations were very similar in elevation. This indicates the variability of snow accumulations throughout the winter range.

Snow depth patterns monitored in permanent plots throughout the moderate winter of 1984/85 indicated that snow accumulations were significantly different between open and canopied habitats. Snow accumulations buried essentially all vegetation in open habitats such as bogs (wetlands), rock outcrops, and young regenerating conifer stands (1- to 20-year-old). No appreciable differences were noticed between snow depths on different aspects in the same habitat types but as a rule, south aspect rock outcrops had slightly decreased snow depths as compared to young regenerating conifer stands (1- to 20-year-old) and bogs. Snow accumulations within deciduous-conifer complexes were more variable because of large differences in canopy closures. Although snow depths were shallower than in more open habitats, they were sufficient to bury forbs and ferns in most instances. Comparisons of snow depths within 21- to 60-year-old conifer stands were also highly variable due to large variations in canopy closures. Snow depths were generally 20 to 50% lower in conifer stands greater than 20 years of age and with more than 60% canopy closure than in open habitats, especially during periods where snow had accumulated over several days. For example, when snow had accumulated to a depth of 30 cm on a rock outcrop, adjacent conifer stands had snow depths of only 15 cm. In conifer stands with backlog spacing debris, snow accumulations were slightly greater. Snow accumulation patterns are illustrated for each habitat type in Figure 5.

Table 9. Permanent snow station data for the 1984/85 winter (mean snow accumulation by month)

Station	Date	n	Mean	SD
Mohun Gravel Pit	November 1984	6	7.96	8.01
Cranberry Junction	November 1984	6	17.08	1.11
Morton Road	November 1984	6	19.25	11.78
Gosling Junction	November 1984	3	17.58	9.17
Loveland Bay	November 1984	4	16.69	8.2
Mohun Gravel Pit	December 1984	14	9.00	6.45
Cranberry Junction	December 1984	10	9.80	8.61
Morton Road	December 1984	10	28.35	4.65
Gosling Junction	December 1984	8	26.78	3.14
Loveland Bay	December 1984	7	18.64	5.3
Mohun Gravel Pit	January 1985	8	4.06	5.64
Cranberry Junction	January 1985	5	4.80	3.67
Morton Road	January 1985	8	24.75	3.41
Gosling Junction	January 1985	6	17.17	5.57
Loveland Bay	January 1985	5	8.9	5.72
Mohun Gravel Pit	February 1985	14	8.52	6.84
Cranberry Junction	February 1985	10	14.37	9.15
Morton Road	February 1985	13	39.59	13.55
Gosling Junction	February 1985	9	31.17	10.88
Loveland Bay	February 1985	8	15.97	5.71
Mohun Gravel Pit	March 1985	3	0	0
Cranberry Junction	March 1985	2	0	0
Morton Road	March 1985	3	32.58	12.05
Gosling Junction	March 1985	2	28.99	4.58
Loveland Bay	March 1985	2	10.37	1.94

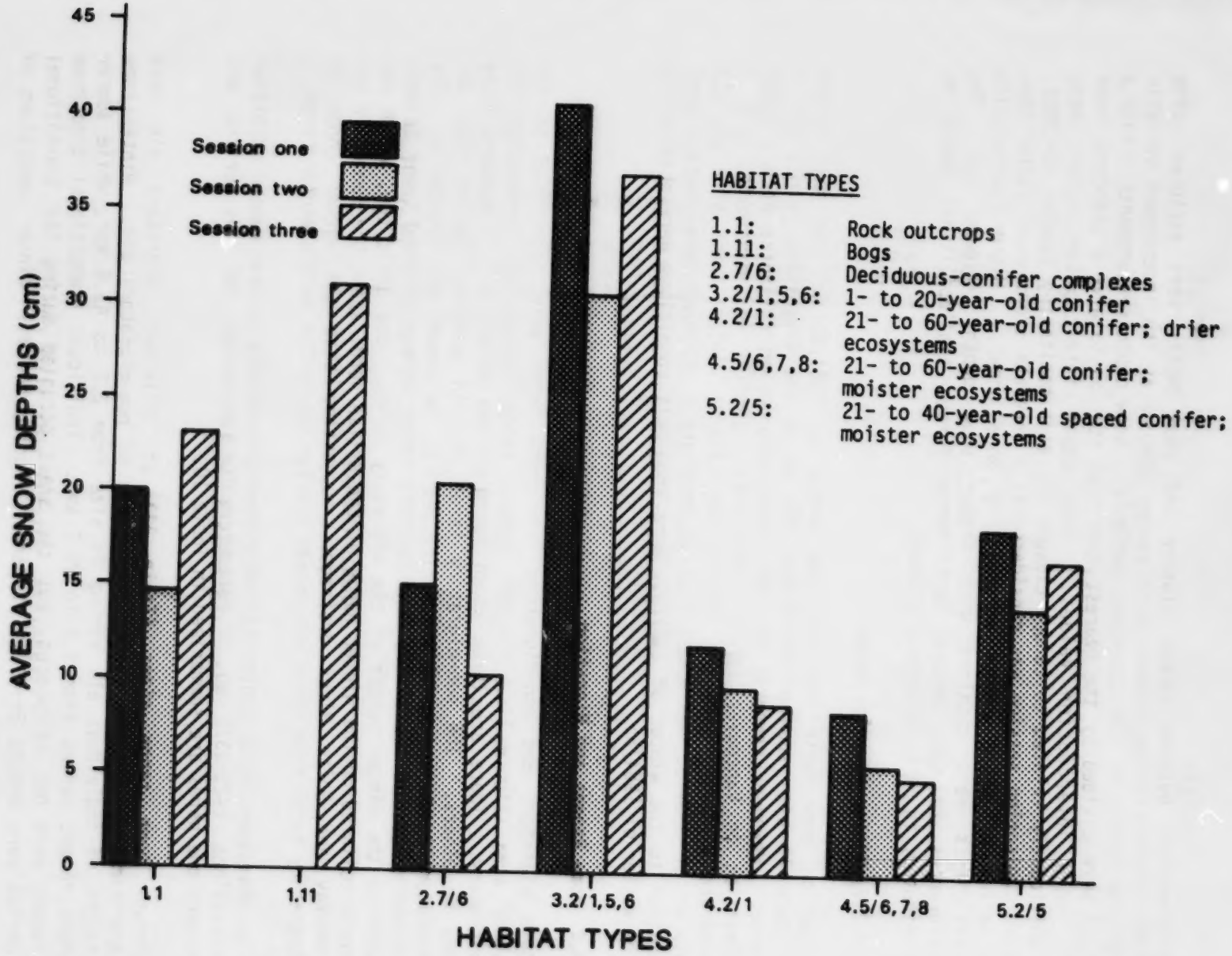


Figure 5. Comparative histogram of various snow depths in each habitat type during different monitoring sessions. (Session four was not included since no data were collected in the various habitat types during that monitoring session.)

Relationships between canopy closure and snow depths were explored using linear regression techniques, with canopy closure as the independent variable and snow depths as the dependent variable. Snow depth measurements within a stand were divided by the nearest open road station to give a standard index for snow interception values. Snow depth interception values were significantly related to canopy closure for each monitoring session ($p<.001$). (Each monitoring session was considered as a separate storm event rather than a series of storm events accumulating more snow). Higher correlation coefficients were obtained with deeper snow depths (Figure 6). The differences in snow depths (and, hence forage availabilities) could be attributed, in part, to canopy closure.

4.2.2.2 Winter severity index

Based on snow depth profiles, the winter of 1981/82 was the most severe (Figure 7) with snow accumulations >60 cm on the Greenstone herd's winter range. However, compared to snow depth information collected at a similar elevation on Vancouver Island (Janz 1983), 1981/82 was considered only a moderate winter. Both the 1982/83 and 1983/84 winters were mild and the winter of 1984/85 was classified as moderate. Although snow depths were similar to the winter of 1981/82, more snow melt conditions were observed in the winter of 1984/85.

4.3 Home Ranges and Migration

Both migratory and non-migratory (resident) herds were identified in the study area (Figure 1). The two largest herds (Grilse and Greenstone) are migratory. There are three known non-migratory herds, but it appears there may be others. The non-migratory herds are, in general, smaller than the migratory herds and spend the entire year at low elevations (50-300 m). The annual ranges of two of the non-migratory herds (Swamp Lake and Lower Salmon) overlap the winter ranges of the migratory herds. One adult cow, which was radio-collared on the winter range of the Grilse herd, spent the summer in the Memekay and White River drainages, suggesting that the winter range of migratory herds from these watersheds overlap the Grilse herd's winter range.

The migratory herds winter at low elevations (90-370 m) and summer at higher elevations (425-1370 m). Parameters of migration for the Grilse and Greenstone herds are summarized in Table 10.

Annual home range sizes (Table 11) of individual migratory elk were approximately 6 times larger than those of non-migratory elk. Winter home ranges of individual elk varied in size from 2.2 to 43.8 km^2, while summer home ranges varied from 3.5 to 29.2 km^2. Individual transitional area home ranges were not calculated, but the areas occupied during the transitional period were around 25-40 km^2 in area. During the mild winter conditions of

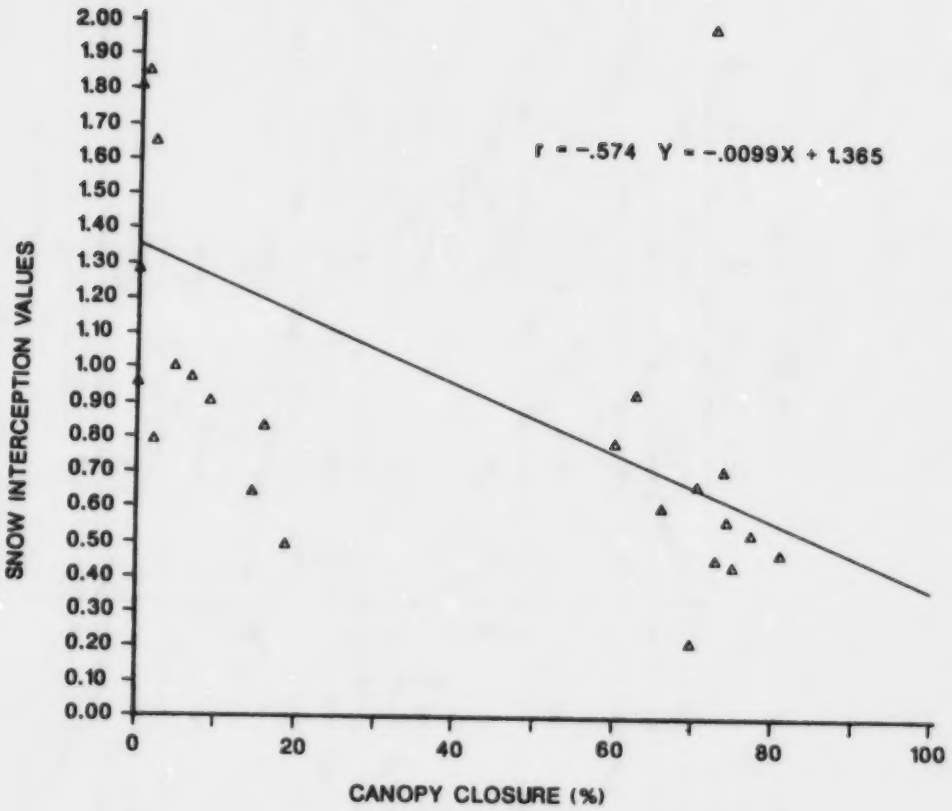


Figure 6. Relationship between snow interception values and canopy closure (%) for the moderate winter of 1984/85.

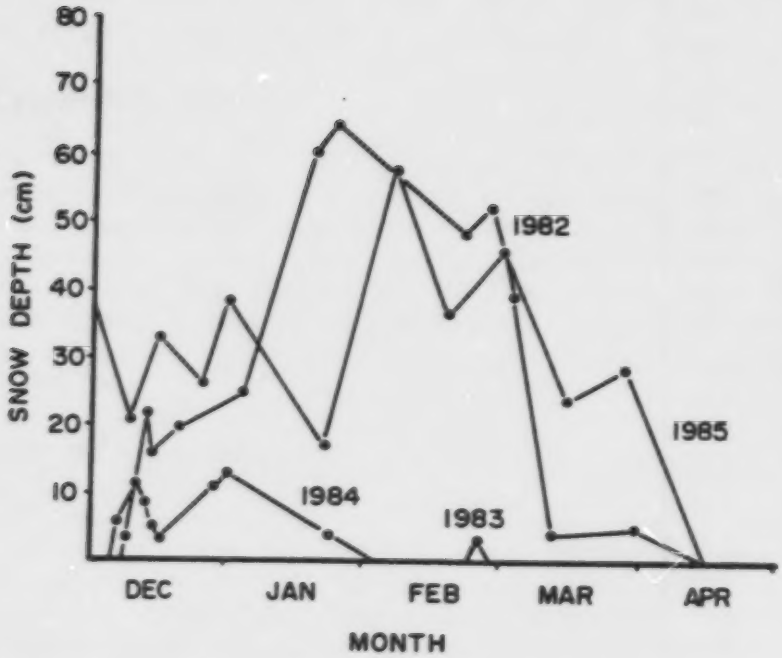


Figure 7. Accumulated snowpack for Mohun Lake (200 m), 1982-1985.

Table 10. Parameters of migration for the Grilse and Greenstone herds

	GRILSE HERD			GREENSTONE HERD		
	Summer range (Grilse Ck. & Gold Lk.)	Winter range (Lower Salmon)	Transitional range (Bootfrog Lk.)	Summer range (Upper Greenstone)	Winter range (Cranberry/Loveland)	Transitional range (Lawson & Patterson Lk.)
ELEVATION (m)	425-660/560-1370	90-370	460-730	850-1070	60-300	180-300
TIME SPENT ON THE RANGE	5-7 months	4-6 months	1-2 months	5-7 months	4-6 months	1-2 months
FORESTRY ACTIVITY	Grilse Creek - approx. 50% of the area logged. Regen. aged 1-10 yrs. No spacing. Gold Lake - undisturbed natural slide area	Approx. 90-95% of area logged. Regen. aged 0-45 years. Limited spacing 10-15 years ago.	Almost totally logged. Regen. aged 10-20 yrs. Moderate amounts of spacing treated 5-8 yrs. ago.	Approx. 50-75% of area logged. Regen. aged 2-10 years. No spacing.	Approx. 95% of area logged. Regen. aged 5-50 yrs. (Most is 35-45 yrs.) Many large blocks of backlog spaced stands treated over the last 5-10 years.	Approx. 90% of area logged. Regen. aged 20-35 yrs. Some large backlog spaced stands treated over the last 5-10 yrs.
MIGRATION DISTANCES (STRAIGHT LINE)	Summer to winter range 18-26 km	Winter to summer range 8 km	Trans. to summer range 10-18 km	Summer to winter range 17 km	Winter to trans. range 8-12 km	Trans. to summer range 5-8 km
COMMENTS	Grilse Creek - wide valley bottom around main drainage creek. Steep walled valley sides of general N and S aspect. Several very large and many smaller bogs interspersed with old growth. Gold Lake - very steep subalpine old growth and/slide alder complex. Mostly N and S aspect.	Very wide (3-5 km) valley bottom with many bogs in Salmon R. flats; gentle slopes with variable aspect elsewhere	Steep E aspect. Some small bogs on flat benches.	Mostly steep E aspect with some bogs on flat benches.	Gentle slopes of variable aspect. Steeper areas S aspect.	Some very large bog (Myrica/Spiraea) areas.

Table 11. Annual and seasonal home range size estimates for adult cows in four herds.

Herd	Animal No.	Home range size (km²)		
		Annual	Summer	Winter
Grilse (migratory)	41	164.4	4.0	6.6
	221	167.1	9.5	30.1
	252	137.1	3.5	43.8
	271	155.5	11.1	19.6
	391	130.5	4.4	
	1038		6.6	2.2
	Mean	150.9	6.5	20.5
Greenstone (migratory)	262	152.1	29.2	9.9
	490[1]	862.6		2.2
	591	266.0		2.8
	641	149.6		9.9
	Mean[2]	189.2		6.2
Lower Salmon (resident)	342	23.7		
Greybe's (resident)	61	10.5		

[1]No. 490 winters with the Greenstone herd, but summers in the Heber River, 42 km away.
[2]The annual home range of No. 490 was excluded from this mean.

the study, winter ranges were generally occupied from November through March, summer ranges from late April through early November, and transitional ranges for varying periods during March/April and October/November. Generally, more time was spent on transitional ranges during spring migration than during the fall. Both winter and summer ranges (all areas generally used by an entire herd) were approximately 30 km^2 in area. Other studies have reported elk summer ranges to be from 1.5 (Hash 1973) to 5 (Craighead *et al.* 1973) times larger than winter ranges. Janz (1983) found elk summer ranges to be 2-3.5 times larger than winter ranges on Vancouver Island. However, the studies cited occurred in either Rocky Mountain interior regions where more severe winters normally occur, or, in the case of Janz (1983), during winters of greater severity than occurred during this study. Waldrip and Shaw (1979) noted no seasonal shifts or changes in home range size and attributed it to mild weather conditions. It is assumed that in the event of a severe winter with significant snowpacks, winter home ranges would be significantly smaller than summer home ranges in the study area. During a severe winter, elk would likely reduce activity to avoid excessive energy expenditures in locomotion, and concentrate use around important areas on the winter range.

Sample size was too small to compare summer range sizes between the Grilse and Greenstone herds, but winter range sizes were not significantly different ($.1<p<.2$) between the two herds.

Migration to the winter range occurred mostly during November even in the absence of snow on the summer range. Transitional ranges were used by the Grilse and Greenstone migratory herds during both the fall and spring migration. Spring migration to the summer range usually took place in April and May and did not generally occur until snowpack on the summer range had mostly disappeared. Elk commonly migrated to the summer range several weeks before the spring flush of vegetation growth. One adult cow (No. 271) repeatedly migrated to the Grilse Creek summer range a month or more before other radio-collared members of the Grilse herd.

Migratory elk benefit from reduced snowpacks on lower elevation winter ranges, and greater forage abundance and diversity on higher elevation summer ranges. The elevation gradient available on summer ranges also provides forage in various stages of phenological development so that succulent forage is available for a longer period than at lower elevations. However, the energetic costs of locomotion are greater to migratory elk. They are also exposed to increased chances of predation or accident while travelling over relatively unfamiliar migratory routes. Because both migratory and non-migratory elk exist in the study area, it appears that patterns of resource availability and weather are sufficiently unpredictable that neither behaviour is used exclusively. However, since migratory herds are generally larger and more numerous, migration appears to offer an advantage in most instances. If the recent pattern of mild winters continues, the need to access higher quality summer ranges may be reduced and a larger portion of

the population may become non-migratory. Increasingly smaller proportions of Roosevelt elk populations are migratory at lower latitudes throughout their range of distribution.

Most radio-collared elk displayed high fidelity to seasonal ranges during the study period. However, several examples of long-distance movement and movements from or between herds occurred during the study. In one case, a 5-year-old cow (No. 490) that wintered with the Greenstone herd, spent the summer and breeding seasons with a different herd (in the Heber River), a straight-line distance of 42 km. This pattern was repeated for 3 years. A 5-year-old cow (No. 332) that was collared on the winter range of the Grilse herd repeatedly spent the summer in the White River. It is unknown whether these cows independently followed these movement patterns or were associated with other elk who migrated as a group between watersheds.

In another example, an 18-year-old cow (No. 252) that spent the summer and winter with the Grilse herd for 3 years, migrated to the Elk River watershed for the mild winter of 1983/84. After 8 months, she returned to her previous range. A 12-year-old cow (No. 1281) that was radio-collared near Brewster Lake in the summer, and was assumed to be from the Swamp Lake herd, wintered on the Greenstone herd winter range where she was illegally killed 17 months after being radio-collared.

Young males appeared to move between watersheds more freely than females. One 2-year-old male (No. 241), captured on the Greenstone herd summer range, was found dead on the Grilse herd summer range 5 months after being radio-collared. A 3-year-old male (No. 371), collared on the Grilse herd summer range, moved to the Elk River and returned to the Grilse herd transitional range where the collar was dropped, all within 4 months of being captured. A 3-year-old male (No. 621) could not be located 14 months after radio-collaring and although collar failure or poaching may have occurred, emigration from the study area is also a possiblity.

4.4 Seasonal Diet Composition

Food habits varied widely between herds and seasons (Tables 12-16, Figures 8 and 9). While elk appeared to feed on a wide variety of available forage species during all seasons, certain plants consistently composed large portions of seasonal diets. Ferns, including deer fern (*Blechnum spicant*) and sword fern (*Polystichum munitum*), and graminoids comprised the bulk of spring foods. Conifers and shrubs were also important as spring foods. During summer, use of conifers declined to 5% or less in all herd diets. Shrubs such as *Rubus* spp., red elderberry (*Sambucus racemosa*), and bunchberry (*Cornus canadensis*) became important during the summer. The use of graminoids remained high in summer, whereas the general use of ferns declined. In the migratory herds during the fall, use of conifers and ferns increased, while the use of graminoids declined. In non-migratory herds,

Table 12. Percent spring diet composition by herd during 1981

SPECIES	Migratory Herds		Non-Migratory
	Grilse	Greenstone	Lower Salmon
Tsuga heterophylla		10.2	6.2
Thuja plicata	1.8	0.8	
Abies amabilis	4.5	6.0	
Taxus brevifolia	14.4		0.4
Total - Conifers	20.7	17.0	6.6
Cornus canadensis	7.9	0.6	0.1
Rubus spp.	7.1	8.7	8.8
Physocarpus capitatus	3.5		3.2
Vaccinium spp.	3.2	3.3	1.5
Sambucus racemosa		0.1	1.1
Alnus rubra	0.2	2.2	0.3
Salix sp.		0.9	
Gaultheria shallon		0.3	
Unknown			4.0
Total - Shrubs	21.9	16.1	19.0
Lysichitum americanum	1.6	0.2	
Linnaea borealis		3.5	
Hypochaeris radicata			1.4
Unknown			2.1
Total - Forbs	1.6	3.7	3.5
Grasses	15.5	14.6	28.5
Carex spp.	6.9	0.8	8.0
Total - Graminoids	22.4	15.4	36.5
Polystichum munitum	7.2	6.4	34.4
Blechnum spicant	26.2	41.3	
Athyrium filix-femina		0.1	
Total - Ferns	33.4	47.8	34.4
Number of identified species	13	17	14
Number of collection days composing sample	4	1	1

Table 13. Percent summer diet composition by herd during 1981

SPECIES	Migratory Herds		Non-Migratory Herds	
	Grilse	Greenstone	Lower Salmon	Greybe's
Tsuga heterophylla	0.6		3.8	1.7
Thuja plicata			1.3	1.2
Abies amabilis	2.0	4.3		
Taxus brevifolia	1.7	0.1	—	—
Total - Conifers	4.3	4.4	5.1	2.9
Cornus canadensis	2.2	0.4		33.9
Physocarpus capitatus	6.8	3.4	4.1	6.8
Rubus spp.	44.3	6.9	2.8	2.6
Sambucus racemosa	23.3		0.7	0.3
Salix sp.			0.5	
Vaccinium spp.	0.1	0.3	1.3	2.3
Gaultheria shallon		0.5		0.1
Ribes sp.	2.1			
Unknown	—	44.0	36.3	—
Total - Shrubs	78.8	55.5	45.7	46.0
Lysichitum americanum	2.3	2.6	5.5	11.7
Mycelis muralis	1.1	7.1	7.3	14.3
Veratrum viride				2.9
Aruncus sylvester				0.4
Hypochaeris radicata		0.2	0.4	
Tiarella trifoliata	—	1.1	—	—
Total - Forbs	3.4	11.0	13.2	29.3
Grasses	9.9	18.1	12.8	8.7
Carex spp.	2.5	6.2	1.2	0.3
Total - Graminoids	12.4	24.3	14.0	9.0
Polystichum munitum		0.9	9.4	2.7
Athyrium filix-femina	0.4		12.5	7.1
Blechnum spicant			0.3	0.6
Unknown		3.8		2.4
Equisetum sp.	0.7	0.2	—	—
Total - Ferns	1.1	4.9	22.2	12.8
Number of identified species	15	17	16	18
Number of collection days composing sample	10	7	4	1

Table 14. Percent fall diet composition by herd during 1981

SPECIES	Migratory Herds		Non-Migratory Herds	
	Grilse	Greenstone	Lower Salmon	Greybe's
Tsuga heterophylla		3.4	11.9	0.6
Thuja plicata	3.0	3.2	12.7	16.1
Abies amabilis	16.7	14.0	0.1	
Total - Conifers	19.7	20.6	24.7	16.7
Rubus spp.	6.3	4.5	8.1	8.9
Cornus canadensis	32.0	5.4	1.6	
Vaccinium spp.	0.4	0.1	1.0	
Alnus rubra			1.4	
Gaultheria shallon	0.4	1.5	0.3	0.3
Physocarpus capitatus	0.1		0.1	
Myrica gale			1.4	
Symphoricarpos sp.		0.6		4.0
Mahonia nervosa		0.3		
Lonicera sp.		3.7		
Unknown			15.0	
Total - Shrubs	39.2	16.1	28.9	13.2
Linnaea borealis	2.9	2.0		2.0
Mycelis muralis	6.1	0.4	15.2	
Epilobium angustifolium	3.6	0.3	0.5	
Lysichitum americanum	3.3	0.3	0.5	
Total - Forbs	15.9	3.0	16.2	2.0
Grasses	0.3	0.2	20.7	62.9
Carex spp.	0.1	0.2	0.6	1.0
Total - Graminoids	0.4	0.4	21.3	63.9
Polystichum munitum	0.4	2.2	4.6	0.1
Blechnum spicant	24.4	57.1	1.7	3.8
Athyrium filix-femina		0.6	2.6	0.3
Total - Ferns	24.8	59.9	8.9	4.2
Number of identified species	15	19	19	11
Number of collection days composing sample	9	2	2	1

Table 15. Percent winter diet composition of migratory herds by year

SPECIES	Grilse Herd		Greenstone Herd					
	Dec-Jan 81/82	Feb-Mar 1982	Dec-Jan 81/82	Feb-Mar 1982	Jan-Feb 1983	Dec-Jan-Feb 83/84	Dec-Jan 84/85	Feb-M 1995
Tsuga heterophylla	4.2	4.2	26.1	13.0	23.9	19.9	22.4	29.6
Pseudotsuga menziesii		0.5				0.9	4.3	1.8
Thuja plicata	14.8	7.1	9.6	40.8	1.2	3.2	6.1	4.9
Abies amabilis	4.3		5.3	1.8				
Taxus brevifolia		1.0						
Pinus spp.						0.1		
Total - Conifers	23.3	12.8	41.0	55.6	25.1	24.1	32.8	36.3
Gaultheria shallon	9.6	9.1	12.1	7.2	3.4	9.0	10.9	12.0
Mahonia nervosa		2.8	3.3	6.0		2.9	4.4	2.0
Vaccinium spp.	4.3	8.4	2.7	8.9	3.1	0.4	13.3	9.2
Arctostaphylos uva-ursi						0.4		0.6
Salix spp.	4.3						0.7	1.5
Alnus rubra	1.5				0.3			
Rubus spp.		1.6			0.9		0.9	1.5
Ribes spp.					0.4		0.3	0.3
Myrica gale					0.5			
Menziesia ferruginea							0.3	0.9
Oplopanax horridus							0.2	
Paxistima myrsinites							0.6	1.1
Rosa gymnocarpa							0.8	
Sambucus racemosa							0.2	1.6
Spiraea douglasii								0.2
Other		1.3	0.5			6.0	0.5	
Total - Shrubs	19.7	23.2	18.6	22.1	8.6	18.7	33.1	30.8
Linnaea borealis	17.2	14.5	22.0	12.6	14.1	19.2	5.6	6.0
Lysichitum americanum					0.9			
Achlys triphylla					0.2			
Mycelis muralis	0.5							
Viola spp.					0.1			
Lycopodium clavatum							0.5	0.7
Other							0.2	0.3
Total - Forbs	17.7	14.5	22.0	12.6	15.3	19.2	6.3	7.0
Grasses	0.7	0.3	8.8	6.8	20.2	9.4	7.0	8.6
Carex spp.		5.3	0.4		11.9	20.0	4.3	8.1
Rushes							0.2	0.6
Total - Graminoids	0.7	5.6	9.2	6.8	32.1	29.4	11.5	17.3
Blechnum spicant	34.1	29.5	6.6	1.6	8.7	5.9	10.1	2.3
Polystichum munitum	4.5	12.2	1.6		2.5	2.3	4.6	0.7
Athyrium filix-femina		1.2	0.6		3.3	0.2	0.7	2.9
Pteridium aquilinum			0.4		0.4		0.2	0.4
Equisetum spp.		0.2			3.8		0.1	1.0
Rhizomes							0.6	1.2
Total - Ferns	38.6	43.1	9.2	1.6	18.7	8.4	16.3	8.4
Lichen		0.8		1.3	0.2	0.2		0.2
Number of identified species composing ≥ 0.2% of diet	12	17	14	10	20	16	27	27
Number of collection days composing sample	14	2	2	4	3	7	7	13

Table 16. Percent winter (1981/82) diet composition of non-migratory herds

SPECIES	Lower Salmon		Greybe's	
	Dec-Jan	Feb-Mar	Dec-Jan	Feb-Mar
Thuja plicata	29.7	12.8	39.9	11.3
Tsuga heterophylla	18.6	14.3	10.7	11.3
Pseudotsuga menziesii		10.2		24.2
Abies amabilis		4.8		1.5
Total - Conifers	48.3	42.1	50.6	48.3
Cornus canadensis		1.8		
Vaccinium spp.	23.2	7.4	15.0	9.5
Mahonia nervosa	8.3		4.8	
Gaultheria shallon	1.7	1.3	11.5	6.2
Alnus rubra	1.4	2.2		
Lonicera involucrata	1.3			
Salix spp.	0.1	9.2		4.8
Total - Shrubs	36.0	21.9	31.3	20.5
Linnaea borealis	5.4	2.9	14.5	
Lysichitum americanum			0.2	13.7
Total - Forbs	5.4	2.9	14.7	13.7
Grasses		1.1	0.4	0.9
Carex spp.		9.8		4.3
Total - Graminoids		10.9	0.4	5.2
Polystichum munitum	10.3	19.1	3.0	4.3
Blechnum spicant		2.2		5.8
Athyrium filix-femina				0.3
Equisetum spp.				0.5
Total - Ferns	10.3	21.3	3.0	10.9
Lichens		0.9		1.4
Number of identified species composing ≥ 0.2% of diet	10	15	9	15
Number of collection days composing sample	3	3	3	2

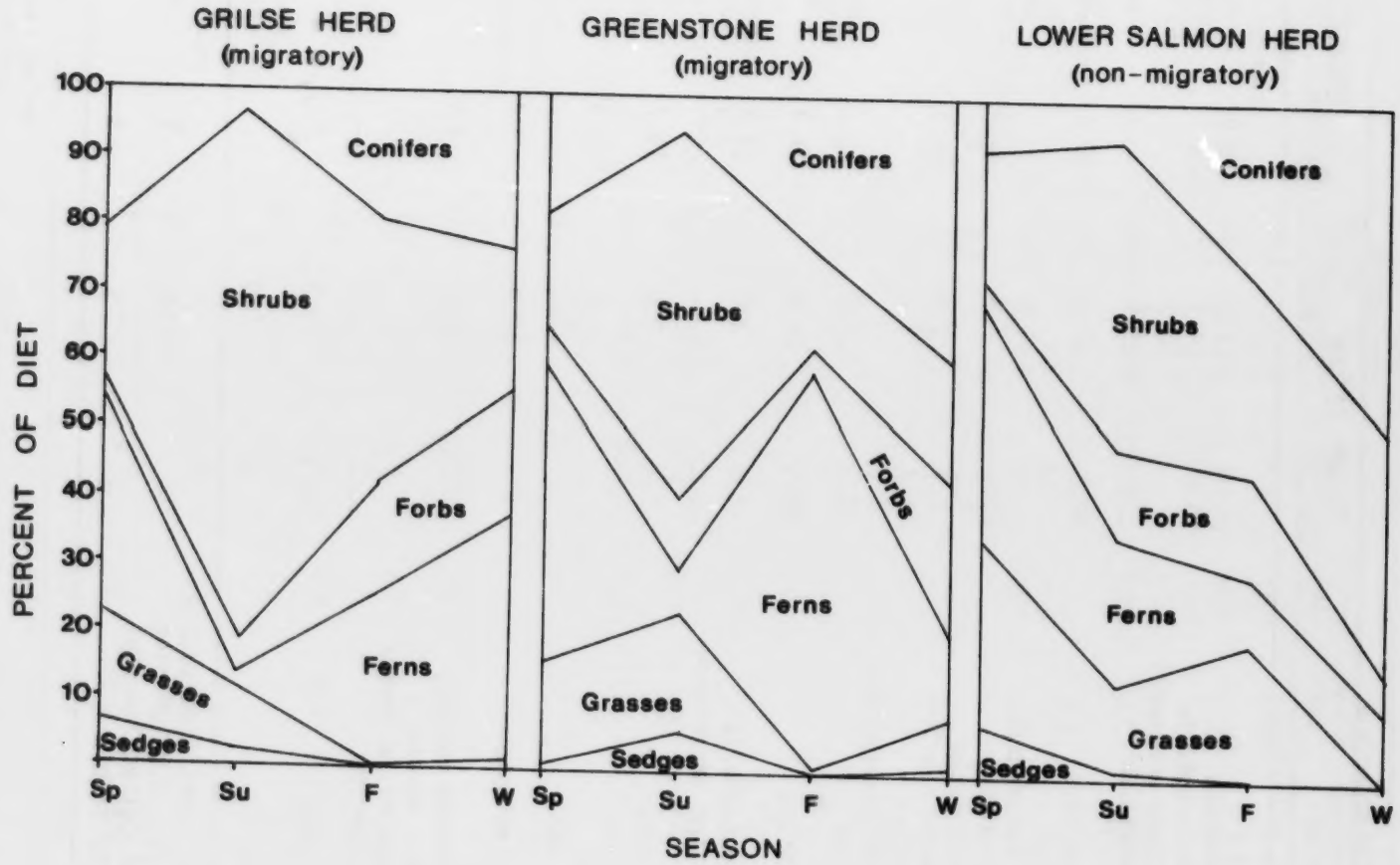


Figure 8. Seasonal diet trends by forage class for three herds from spring 1981 through winter 1982.

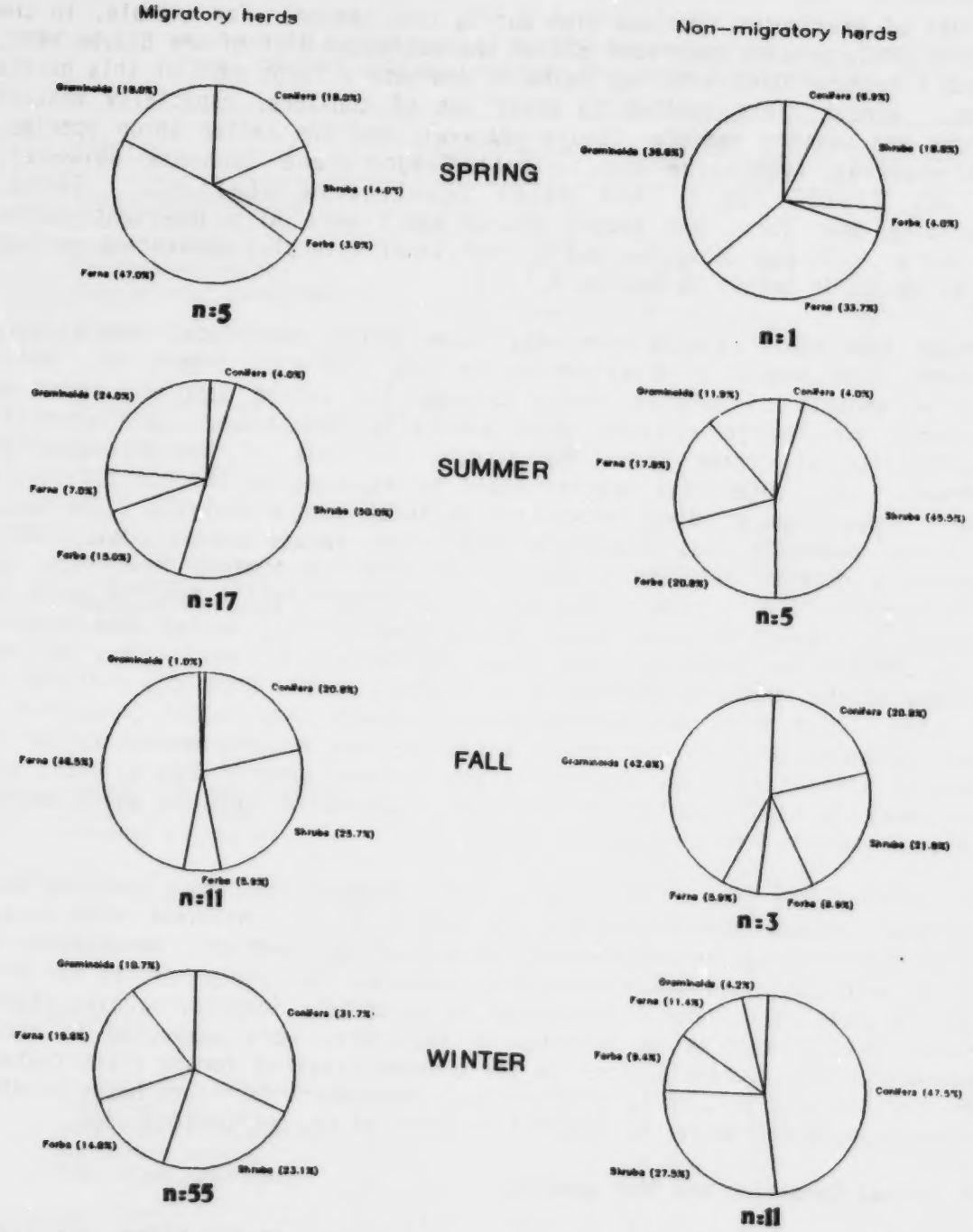


Figure 9. Seasonal diet composition by forage class of migratory (Grilse and Greenstone) and non-migratory (Lower Salmon and Greybe's) elk herds from March 1981 through March 1985 (n = number of collection days composing sample).

the use of graminoids remained high during this season. For example, in the fall of 1981, grasses comprised 63% of the estimated diet of the Greybe herd, probably because farms with hay pastures dominate a large part of this herd's range. Winter diets shifted to heavy use of conifers, especially western hemlock and western redcedar (*Thuja plicata*), and the taller shrub species, huckleberries (*Vaccinium* spp.), dull Oregon-grape (*Mahonia nervosa*), willows (*Salix* spp.), and salal (*Gaultheria shallon*). Ferns, especially deer fern, and sedges (*Carex* spp.) were also important during the winter. Forage selection during individual intensive monitoring periods are discussed in detail in Section 4.7.4.2.

Although food habit results from only three paired rumen/fecal samples were compared, some general observations can be made (Table 17, Figure 10). While relative amounts of species varied between the paired samples, ranks of abundance of forage classes were generally the same. Differential digestibility of forage items may account for some of the discrepancies observed. Less digestible species would be expected to compose relatively greater proportions of diets determined by fecal sample analysis. Conifers, which are generally less digestible than other forage groups (Janz 1983), composed a greater relative proportion of diets determined from fecal vs rumen samples in each case. Even greater discrepancies in results would be expected in seasons or areas where forage digestibility varied more widely. It is unknown how much care was taken by hunters to sample from various portions of the rumen, as opposed to selecting a sample from only one area of the rumen, which might not realistically represent food intake throughout a recent foraging bout by the elk. While the two methods appear to derive generally similar results, feeding trials, a much greater sample size, and consistency in sample collection would be required to conclude which method more accurately reflects actual elk diets.

Some seasonal diet results obtained by fecal fragment laboratory analyses were questioned because the values did not appear to be consistent with forage species availability on the seasonal range that was sampled. Re-analyses by the lab were conducted and alternatives named as the likely species for diet items in question. These difficulties in accurately identifying diet items, because of similarities in microscopic structure, were suspected to occur frequently. Diet determinations to the broader level of forage class (rather than species) were felt to be more precise. Management decisions based on diet analyses should recognize the inherent problems of the methodology used.

4.5 Animal Condition and Diet Quality

Three indices of animal condition were used in the study: kidney fat index (KFI), values from hunter-killed elk, fecal crude protein (FCP) levels from fresh fecal samples, and diaminopimellic acid (DAPA) levels, also from fresh

Table 17. Percent fall diet composition as determined by paired rumen and fecal content analysis methods for three hunter-killed elk

SPECIES	Elk No. 1		Elk No. 2		Elk No. 3	
	Rumen	Fecal	Rumen	Fecal	Rumen	Fecal
Tsuga heterophylla	19.0	23.5		0.3	2.5	4.9
Thuja plicata	19.0	26.3	0.1	3.1	9.0	27.8
Abies amabilis	5.2	3.4		1.5		
Taxus brevifolia			0.2	0.8	0.3	
Pseudotsuga menziesii					19.9	27.5
Conifers - Total	43.2	53.2	0.3	5.7	31.7	60.2
Rank	1	1	5	5	2	1
Mahonia nervosa	10.8	5.7	0.7		0.1	
Gaultheria shallon	7.5	1.1				
Alnus rubra	0.7	0.2				
Vaccinium spp.	0.2	0.7	0.3	0.7	1.6	4.0
Salix spp.	0.1					
Rubus spp.	0.3		15.1	15.5	48.1	12.1
Rubus spectabilis			5.4	7.7		
Rubus parviflorus			2.1	0.8		
Physocarpus capitatus			0.9	2.1	1.7	1.4
Sambucus racemosa				1.1	0.2	
Cornus canadensis	1.3		2.4	0.2		
Shrubs - Total	20.9	7.7	26.9	28.1	51.7	17.5
- Rank	3	3	2	2	1	2
Linnaea borealis	7.3	3.4			1.1	
Mycelis muralis	0.1		0.3	0.5	4.3	3.8
Lysichitum americanum			7.5	16.1		
Veratrum viride			0.2			
Aruncus sylvester						1.8
Forbs - Total	7.4	3.4	8.0	16.6	5.4	5.6
Rank	4	4	3	4	4	4
Grasses	0.6	1.3	3.5	17.4	3.3	4.5
Carex spp.	0.6		trace	1.5	0.1	0.2
Graminoids - Total	1.2	1.3	3.5	18.9	3.4	4.7
- Rank	5	5	4	3	5	5
Polystichum munitum	23.4	29.0	1.3	1.6	5.8	10.8
Blechnum spicant	3.9	5.4	56.7	23.1	0.8	
Athyrium filix-femina			1.7	3.7	1.1	
Equisetum spp.			1.6	2.3	0.1	trace
Pteridium aquilinum						1.2
Ferns - Total	27.3	34.4	61.3	30.7	7.8	12.0
- Rank	2	2	1	1	3	3

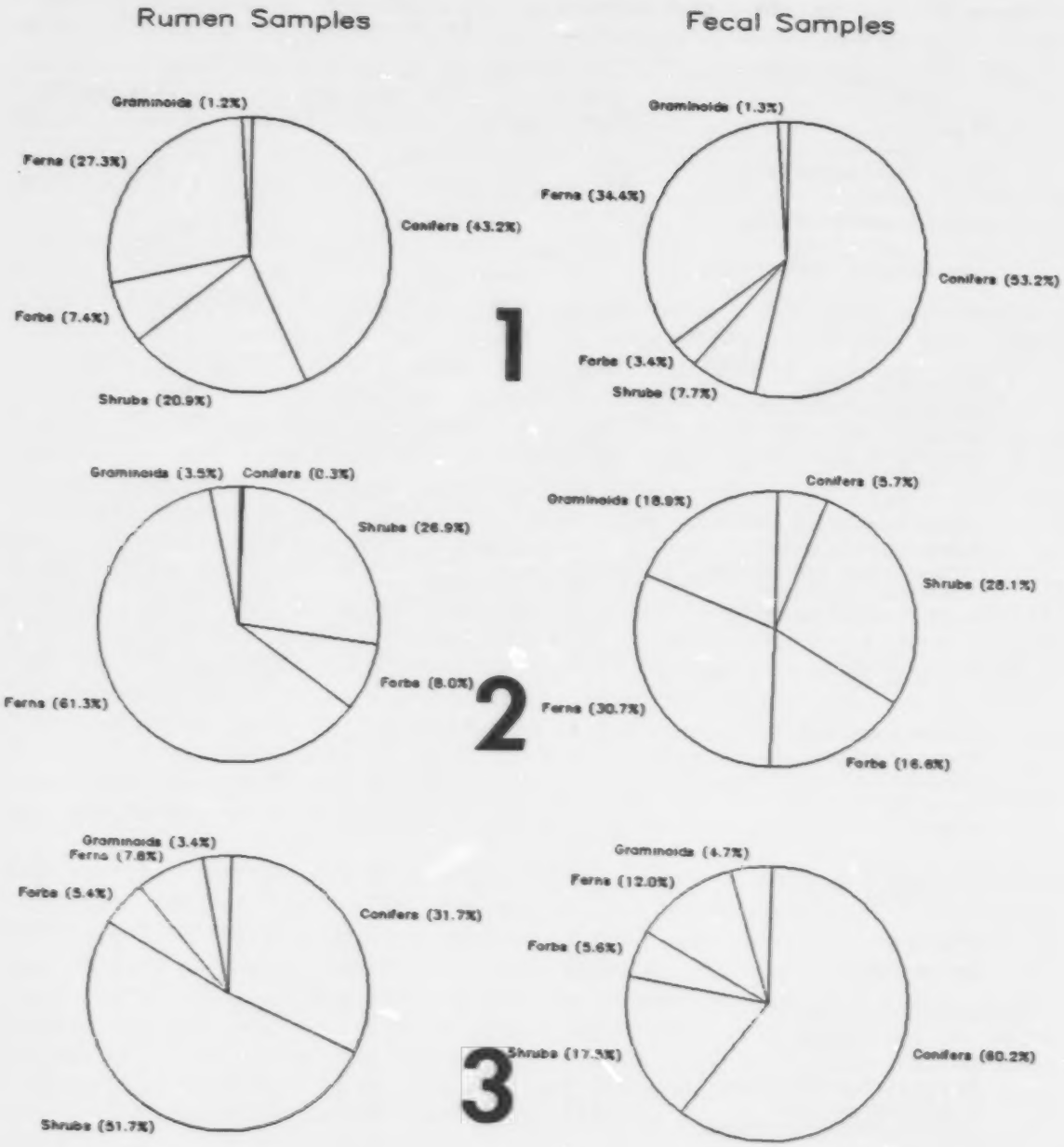


Figure 10. Diet composition by forage class of three hunter-killed elk as determined by paired rumen and fecal sample content analysis methods.

fecal samples. Diet quality was estimated from FCP and DAPA levels. Fall KFI values from hunter-collected elk were lower in 1982 than 1981, but increased annually through 1985 (Table 18). Blood and Smith (1984) noted mean late winter KFI values of 48.3 (n=4) for adult females following a relatively mild winter, and values of 4.5 (n=4) following the severe winter of 1968/69 when winter kills of both deer and elk on Vancouver Island were widespread (G.W. Smith, B.C. Ministry Environment, pers. comm., May 1986). The decline in the KFI from 1981 to 1982 noted in this study corresponded with a winter severity index value from the previous winter that was higher than any other recorded during the study. This suggests that a severe winter may have long-term influences on an elk population. A certain number of elk might be expected to succumb during, or at the end, of a severe winter. However, these data suggest that elk might not be able to replace fat reserves fully during the summer/fall growing season and may enter the winter following a severe winter with less than optimum body reserves. Jones and Mason (1983) noted that female black-tailed deer productivity on northern Vancouver Island was reduced following two severe winters. Productivity gradually increased for 4 years after one of these winters. Similar to results reported by Mech *et al.* (1987) for moose and white-tailed deer, consecutive severe or moderately severe winters probably have a cumulative effect on fall fat reserves, winter survival, and productivity of elk herds on Vancouver Island.

The interpretations of the KFI values presented here must consider the extremely restrictive sample size available (60 samples over 5 years). Anderson *et al.* (1972) determined sample size requirements for a precision of $\pm$ 10% at the 95% confidence level for KFI of mule deer. They noted a requirement of 114 female and 88 male samples. Variability in the manner of collection by hunters of the samples analysed for this study must also be considered. The small sample size, along with variability in method of collection, precludes detailed statistical analyses of the results.

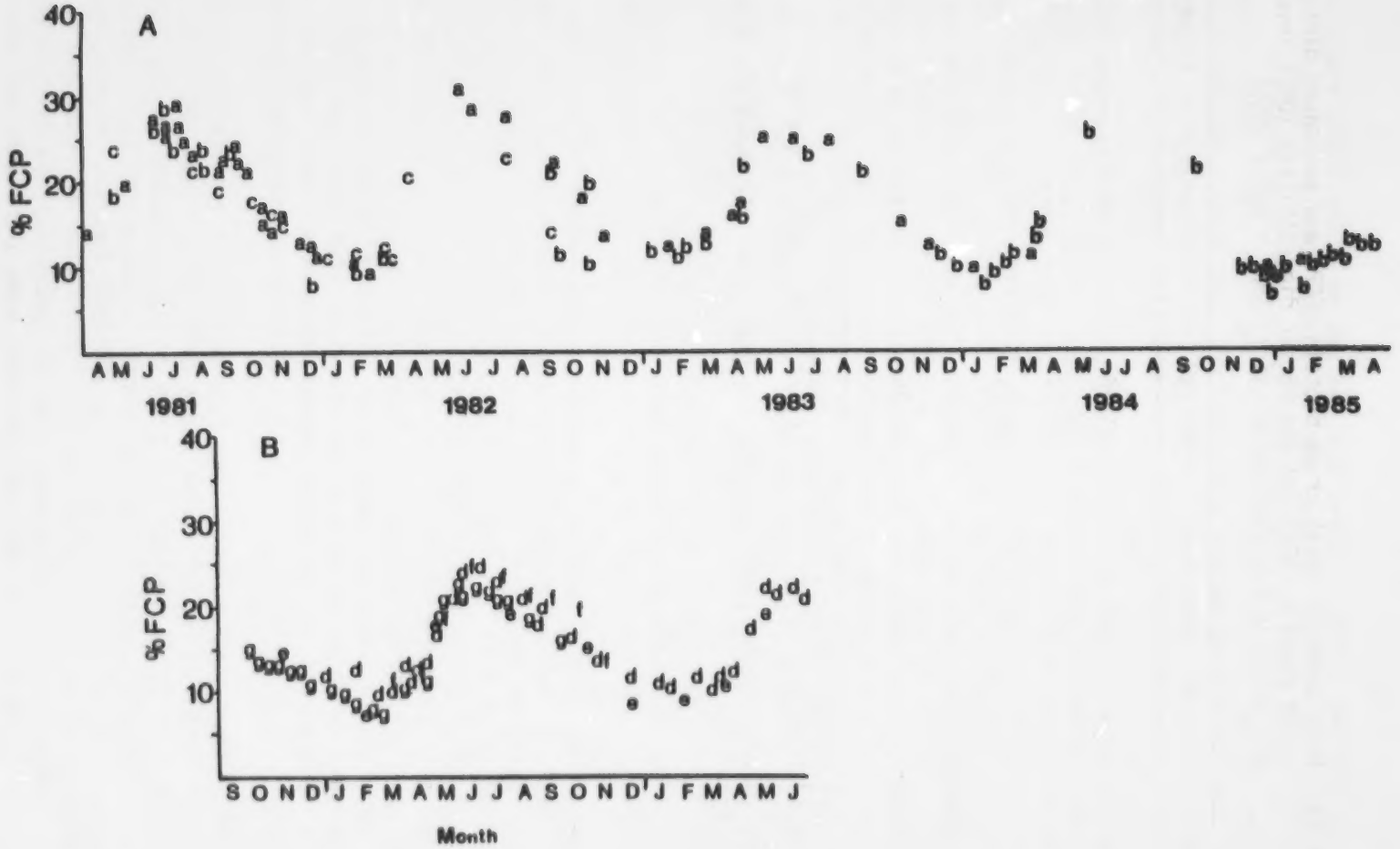
Fecal crude protein (FCP) values showed a seasonally fluctuating pattern, peaking in spring and declining to lowest values in winter, comparable to other studies (Gates 1980; Hanley 1980; Leslie 1982; Janz 1983) (Figure 11). However, FCP peak values were higher than those reported in other studies. The minimum winter values were similar to those reported by Janz (1983) during mild and moderate winters. Using the regression developed by Janz (1983) for estimating dietary crude protein (DCP) from FCP, elk in the study area were obtaining winter forage with crude protein (CP) levels averaging 8.0% (Table 19). These values are well in excess of the minimum 5% requirement suggested by Mould and Robbins (1981) for maintenance.

The FCP levels during early and late winter periods were virtually identical (Table 19), probably as a result of the relatively mild and constant weather conditions that occurred throughout the winters examined. During a period of extended snowpack when relatively higher nutrient quality grasses, shrubs,

Table 18. Winter severity, animal condition indices (KFI = kidney fat index from adult cows; FCP = fecal crude protein; DCP = estimated dietary crude protein), and population parameters from this study (all herds 1981-1985) and Janz (1983).(1975-1978)

Year	Winter Indices (previous Dec. through current March)			Calves:100 cows		
	Winter severity index	Winter FCP (%)	Winter DCF[1] (%)	Early spring	Summer	Mean fall KFI (n)
1981	<1.0	--	--	--	47.5	104.9(17)
1982	15.3	11.9	8.4	31.5	49.0	46.5(18)
1983	0.2	11.5	8.2	41.5	46.0	103.4(17)
1984	1.6	10.5	7.4	35.0	45.5	112.2(3)
1985	15.0	10.7	7.6	52.8	51.5	165.4(5)
1975	38.0	9.1	6.5	13.0	13.0	--
1976	7.8	11.5	8.2	33.0	33.0	--
1977	1.0	11.6	8.2	44.6	44.6	61.3(2)
1978	7.4	11.0	7.8	41.5	41.5	71.0(2)

[1]from Janz (1983); DCP = 0.71 x FCP.


A
% FCP
40
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A M J J A S O N D J F M A M J J A S O N D J F M A M J J A S O N D J F M A M J J A S O N D J F M A
1981
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% FCP
40
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S O N D J F M A M J J A S O N D J F M A M J
Month

Figure 11. Fecal crude protein profiles for (A) the herds in this study (a = Grilse, b = Greenstone, c = Lower Salmon) and (B) other elk studies (d = Janz [1983], e = Leslie [1982], f = Hanley [1980], g = Gates [1980]).

Table 19. Mean seasonal fecal crude protein (FCP) and estimated dietary crude protein (DCP) and dry matter digestibility (DMD) levels for all herds in the study area (April 1981 - March 1985)

Season	n[1]	FCP (%)	DCP[2] (%)	DMD[3] (%)
Spring	14	21.16	15.0	41.7
Summer	28	24.70	17.5	44.7
Fall	21	18.69	13.3	39.6
Early Winter	40	11.28	8.0	33.3
Late Winter	30	11.25	8.0	33.3

[1]Number of collection days composing sample.
[2]Estimated from Janz (1983): $Y = 0.71X$; $r^2 = .95$; where Y = % DCP and X = % FCP.
[3]Estimated from Janz (1983): $Y = 23.7 + 0.85X$; $r^2 = .76$; where Y = % DMD, and X = % FCP.

and ferns (Janz 1983) would be buried, FCP would probably decline as diets contained relatively higher levels of low quality coniferous forage. If persistent snowpacks occurred during late winter when body reserves are at their lowest annual level, poor quality diets would further deplete reserves, which could lead to starvation. Periodic late winter die-offs of elk during severe winters have been noted on Vancouver Island (D.W. Janz, B.C. Ministry of Environment, pers. comm., July 1986).

Janz (1983) measured seasonal crude protein (CP) levels of major elk forage species and found that shrubs averaged 7.6% CP and conifers 6.8% CP in winter. It was suspected that the relatively higher FCP values noted here might be a result of high levels of phenolic compounds, including tannins, in forage species. These compounds function as anti-herbivore devices by forming indigestible complexes with proteins and enzymes, thereby increasing the nitrogen content of fecal samples (Mould and Robbins 1981). Conifers possessed tannin levels higher than those of any other winter forage type sampled (Table 20). If tannin content of winter forage was elevating winter FCP levels, a relationship between the relative conifer content of diet and fecal N might be expected. However, there was no significant relationship ($p>.50$) between conifer content of the diet and fecal N level in 15 fecal sample collections from the Greenstone herd during the winter of 1984/85. Tannin content of winter diets was not considered to be artificially elevating fecal N levels, and the estimated dietary protein levels observed are apparently due to a relatively high protein diet obtained by elk in the study area.

Diaminopimellic acid (DAPA) values showed a seasonal trend similar to FCP, except that DAPA values appear to peak about 1 month earlier in three of four herds sampled compared to FCP (Figure 12). Estimated seasonal diet dry matter digestibility (DMD) and digestible energy (DE) from fecal DAPA levels for four herds during the period May 1981-March 1982 are presented in Table 21. The DE content of diets obtained by non-migratory herds reached their lowest levels in early winter and increased somewhat during the late winter. However, migratory herd DE levels were lower in late winter than early winter. This may have been a result of a slightly earlier greenup which occurred on the lower elevation ranges occupied in the winter by non-migratory compared to migratory herds.

Using the regression for estimating diet DMD from FCP (Janz 1983) (Table 21), seasonal diet DMD levels from this study were similar to those reported by Janz (1983) who estimated values of 45.0% for spring, 42.3% for summer, 34.9% for fall, and 32.5% for winter. Sample collection dates probably account for the annual peak in seasonal diet DMD occurring in the spring rather than the summer, as was noted in this study. Of the three collection dates comprising Janz' sample, one was collected in late June (classified as summer in this study), and the other two were from mid-May and early June. Many of the

Table 20. Tannin (mg/g) content of species collected on the Greenstone winter range in January 1984

	SPECIES	PLANT PART	TANNIN (mg/g)
Conifers	*Pinus contorta*	bark	8.33
	Picea sitchensis	stems and needles[1]	4.11
	Tsuga heterophylla	stems and needles	4.01
	Pseudotsuga menziesii	stems and needles	3.04
	Thuja plicata	stems and needles	2.72
	Pinus monticola	stems and needles	2.11
Mean - Conifers		stems and needles	3.20
Shrubs	*Salix* sp.	bark	5.29
	Alnus rubra	bark	3.13
	Gaultheria shallon	stems and leaves	2.72
	Rubus ursinus	stems and leaves	2.58
	Salix sp.	stems	2.22
	Myrica gale	stems	0.76
	Alnus rubra	stems	0.56
	Rosa gymnocarpa	stems	0.53
	Mahonia nervosa	stems and leaves	0.44
	Rubus spectabilis	stems	0.40
	Vaccinium parvifolium	stems	0.15
	Oplopanax horridum	stems	0.11
Mean - Shrubs		stems and leaves	1.05
Forbs	*Cornus canadensis*	leaves	2.15
	Linnaea borealis	stems, leaves & stolons	0.16
Mean - Forbs			1.16
Ferns	*Polystichum munitum*	fronds	1.01
	Blechnum spicant	fronds	0.63
Mean - Ferns			0.82
Graminoids	*Juncus* sp.	stems and leaves	0.60
	Carex sp.	stems and leaves	0.45
	Luzula sp.	stems and leaves	0.44
	Grasses	stems and leaves[2]	0.22
Mean - Graminoids			0.43

[1]Stems of shrubs and trees were the terminal 8-10 cm of stem.
[2]Stems and leaves of grasses collected were a mixture of dead (brown) and green material.

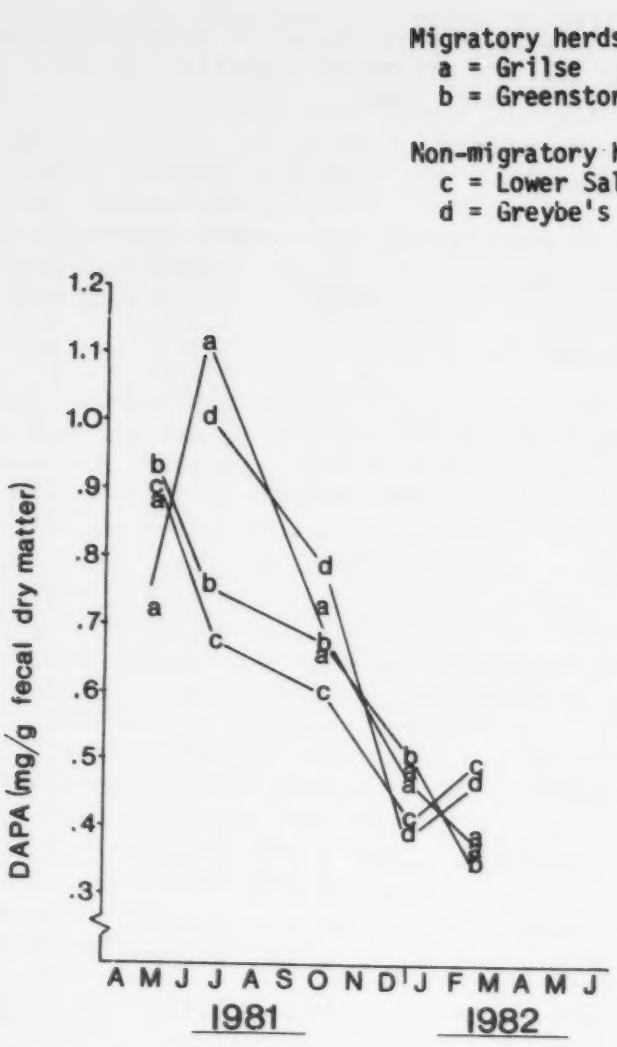

Figure 12. Diaminopimellic acid (DAPA) profiles for four herds in the study area.

Table 21. Fecal DAPA (2, 6 diaminopimellic acid) and estimated digestible energy (DE) and dry matter digestibility (DMD) levels of elk diets (May 1981 - March 1982)

Herd	Season[1]	DAPA (mg/g)	DE[2] (%)	DMD[3] (%)	DMD[4] (%)
Grilse (migratory)	Spring	0.8808	56.2	58.0	
	Spring (Bootfrog Lake)	0.7201	51.5	53.2	
	Summer	1.1163	63.2	65.1	
	Summer (Gold Lake)	0.9653	58.7	60.5	
	Fall	0.7263	51.7	53.4	
	Fall (Gold Lake)	0.7511	52.4	54.1	
	Fall (Bootfrog Lake)	0.6596	49.7	51.3	
	Early winter	0.4813	44.5	46.0	
	Early winter (Bootfrog Lk)	0.4843	44.6	46.1	
	Late winter	0.3733	41.3	42.8	
Greenstone (migratory)	Spring	0.9390	58.0	59.8	
	Summer	0.7549	52.5	54.2	
	Fall	0.6621	49.8	51.4	
	Early winter	0.4969	44.9	46.4	
	Late winter	0.3605	40.9	42.4	
Lower Salmon (non-migratory)	Spring	0.8935	56.6	58.4	
	Summer	0.6667	49.9	51.5	
	Fall	0.6049	48.1	49.7	
	Early winter	0.4148	42.5	44.0	
	Late winter	0.5048	45.2	46.7	
Greybe's (non-migratory)	Summer	1.0372	60.8	62.7	
	Fall	0.7864	53.5	55.2	
	Early winter	0.4044	42.2	43.7	
	Late winter	0.4731	44.2	45.7	
Combined Mean	Spring	0.8584	55.6	57.4	41.7
	Summer	0.9081	57.0	58.8	44.7
	Fall	0.6984	50.9	52.6	39.6
	Early winter	0.4563	43.8	45.3	33.3
	Late winter	0.4277	42.9	44.4	33.3

[1]Spring = Apr. 1-June 14; Summer = June 15-Sept. 14; Fall = Sept. 15-Nov. 14; Early winter = Nov. 15-Jan. 31; Late winter = Feb. 1-March 31.
[2]From B. Davitt (pers. comm., April 1987): $Y = 30.328 + 29.424X$; $r = .95$; where Y = %DE, and X = DAPA (mg/g).
[3]From Mould and Robbins (1982): $Y = -0.61 + 0.98X$; $r^2 = .98$; where Y = %DE, and X = %DMD.
[4]From Janz (1983): $Y = 23.7 + 0.85X$; $r^2 = .76$; where Y = % DMD, and X = %FCP; for all herds in the study area April 1981 - March 1985.

spring samples analysed in this study were collected in April when FCP levels were still relatively low.

Estimated seasonal diet DMD from DAPA data (Table 21) yielded consistently higher values than estimates from FCP levels. However, the regression used to estimate DMD from DAPA data was developed from feeding trials using mule deer (B. Davitt, pers. comm., April 1987). An earlier regression from feeding trials using sheep and cattle (B. Davitt, pers. comm., June 1986) yielded significantly different diet DMD estimates. Subsequent trials using elk will produce a relationship for estimating elk diet DMD levels with more confidence.

Ammann *et al.* (1973) suggested that it is unlikely a ruminant could maintain itself on a diet that was much below 50% DE (51.6% DMD). Estimating diet DMD from FCP using the regression developed by Janz (1983) did not yield values in excess of 45% even at its highest annual level in either this or Janz' study. Therefore, the method of determining diet DMD from DAPA levels may yield more accurate estimates of actual diet DMD. Regardless of the methodology used, energy available to elk from forage is well below maintenance requirements even during a mild winter. This deficit is expected to be even greater during severe winters when snow would bury much of the vegetation in open-canopied, forage-producing areas such as bogs, clearcuts, and deciduous-conifer complexes. These areas typically produce abundant low-growing forage species. Snowpacks would force elk to include greater proportions of tall shrub and conifer browse in their diet, which have lower protein and digestibility levels than most ferns, grasses, and forbs (Janz 1983). The availability of high quality forage is expected to be a critical limiting factor to elk during severe winters.

4.6 Population Characteristics

4.6.1 Calf production

Calf production, as indexed through summer calf:cow ratios, was comparable between the Grilse and Greenstone herds in 1982 and 1984, but not in 1983 and 1985 (Table 22). The decreased calf:cow ratios in the Grilse herd may have been due to increased wolf predation on calves during the summers of 1983 and 1985. Surveys indicated a higher density of wolf scats on the Grilse herd summer range than on the Greenstone herd summer range.

Comparison of calf:cow ratios collected in the study area with those from other studies (Harn 1960; Follis and Spillet 1974; Kimball and Wolfe 1979; Kuttel 1975; Janz 1980) indicated no major differences (Table 23).

Examination of reproductive tract samples from cow elk 2.5 years and older harvested in the study area indicated that 13 of 17 were pregnant. In a larger sample from Vancouver Island, including samples from the study area

Table 22. Summer calf:cow ratios for the Grilse and Greenstone herds

Year	Herd	Number classified	Adult bulls	Yearling bulls	Cows	Calves: 100 cows Calves	80% CI[1]	Mean
1982	Grilse	121	5	7	73	36	47-51	49
	Greenstone	69	6	5	39	19	44-53	49
1983	Grilse	131	4	9	86	32	35-39	37
	Greenstone	72	1	4	43	24	52-60	56
1984	Grilse	143	8	10	86	39	44-46	45
	Greenstone	67	8	5	37	17	40-52	46
1985	Grilse	97	8	6	58	25	41-45	43
	Greenstone	60	2	6	33	19	54-60	57

[1]80% confidence interval

Table 23. Comparative summer calf:cow ratios from this and other studies

Author	Location	Subspecies	Calves: 100 cows n[1]	80% CI	Mean
Harn	N. California	*roosevelti*	5	1-59	30
Follis and Spillett 1974	Utah	*nelsoni*	2		54
Kimball and Wolfe 1979	N. Utah	*nelsoni*	9	47-55	51
Kuttel 1975		*roosevelti*	4	22-85	54
Janz 1980	Vancouver Island	*roosevelti*	5	43-55	49
This study	Vancouver Island	*roosevelti*	7	44-57[2]	50
			8	40-58[3]	49

[1]Represents the number of calf:cow ratios estimated (from one or several herds for one or several years).
[2]Exluding Grilse herd values in 1983.
[3]Including Grilse herd values in 1983.

(n=76), pregnancy rates of 85.5% for cows 2.5 years and older were estimated over a period of relatively mild winter conditions (Janz and Becker 1986). These data are comparable to the 83.8% pregnancy rate for mature cows (≥ 2.5 years) as reported by Kuttel (1975) in southwestern Washington and higher than rates reported in the Olympic Mountains of Washington (61.3%; Smith 1980) and western Oregon (50.0%; Trainer 1971). Age-specific pregnancy rates of cow elk on Vancouver Island are listed in Table 24 (Janz and Becker 1986). Although bull:cow ratios are not included (due to insufficient sample size, see Section 4.6.3), it appears that the quantity of bulls is sufficient for breeding purposes.

Conception dates, estimated from fetal sizes and kill dates (Trainer 1971) ranged from September 10 to October 16 for the study area (n=13). In a combined sample (n=65) from Vancouver Island, conception dates ranged from September 10 to November 30, with the mean conception date as September 28 and the median conception date as September 24 (Figure 13A). Assuming a gestation period of 255 days (Cowan and Guiget 1965), parturition occurred between May 8 and July 6, with a mean birth date of June 2 and median birth date of May 26 (Figure 13B).

In comparison, estimated mean and median conception dates of Roosevelt elk collected in western Oregon (Trainer 1986) differed little from the data from Vancouver Island (Table 25). The spread between the earliest and latest conception dates was slightly larger for the Vancouver Island elk. This variability may be due to the samples being collected from different geographic locations (watersheds all over Vancouver Island) rather than one localized area. Estimated mean and median conception dates of Rocky Mountain elk samples collected in northeastern Oregon (Trainer 1986) indicated conception dates later in the breeding season than samples from Vancouver Island. Trainer (1986) suggests differences in the subspecies, geographic location, body condition, or lack of mature bulls for breeding as possible reasons for the discrepancies.

4.6.2 Survival

Spring calf:cow ratios (Table 26) appeared to correlate with previous winter severity indices ($p<.02$) when the 1984 Grilse herd value was excluded from the calculations for the period from 1982 to 1984. The Grilse herd value was not expected to fit this relationship as it was already depressed during the previous summer, possibly because of predation. With additional data from Janz (1983) included, spring calf:cow ratios were significantly related to winter severity, both including 1984 Grilse herd values ($p<.005$; $r^2=.69$), and excluding them ($p<.0005$; $r^2=.94$) (Figure 14).

The winter of 1984/85 was classified as a moderate winter similar to the winter of 1981/82, based on the winter severity index (Section 4.2.2.2). However, the following 1985 spring calf:cow ratios remained relatively high. Calves

Table 24. Pregnancy rates of cow elk on Vancouver Island 1977-1984 (adapted from Janz and Becker 1986)

Age	No. uteri examined	No. pregnant	% pregnant	Grouped pregnancy rates
1.5	5	0	0	79.5 (ages 2.5-4.5)
2.5	11	9	81.8	
3.5	19	15	78.9	
4.5	9	7	77.8	
5.5	3	3	100.0	100.0 (ages 5.5-9.5)
6.5	4	4	100.0	
7.5	2	2	100.0	
8.5	2	2	100.0	
9.5	5	5	100.0	
10.5	3	2	66.7	85.7 (ages 10.5 onwards)
11.5	3	2	66.7	
12.5	3	3	100.0	
13.5	2	2	100.0	
14.5	1	1	100.0	
15.5	2	2	100.0	
16.5	1	1	100.0	
Adult	6	5	83.3	
TOTAL	81	65	80.0	

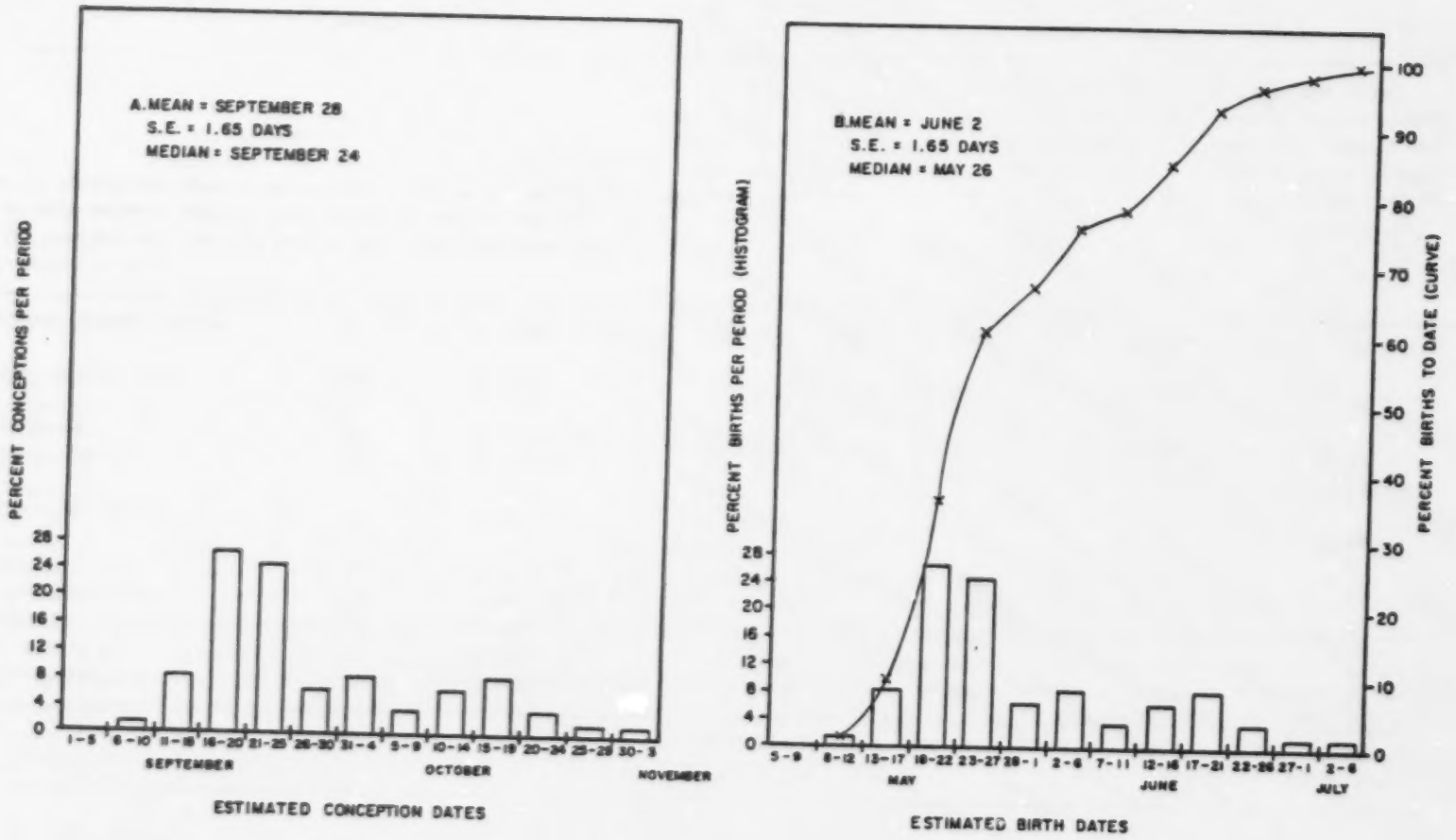

Figure 13. Estimated conception (A) and parturition (B) dates for Roosevelt elk on Vancouver Island (from Janz and Becker 1986).

Table 25. Estimated conception dates of elk samples collected in Oregon during November-January, 1983-1985 (adapted from Trainer 1986) and Vancouver Island during October-January, 1977-1984

Area	n	Mean±SE[1]	Median[2]	Earliest	Latest	Spread in days[3]
Wenaha-Snake River	195[4]	27 Sept. ±0.8	26 Sept.	5 Sept.	1 Nov.	57
North Beulah	83	28 Sept. ±1.1	27 Sept.	4 Sept.	20 Oct.	46
Chesnimnus	50	5 Oct. ±1.7	4 Oct.	12 Sept.	28 Oct.	46
Starkey-Desolation	322	4 Oct. ±0.7	3 Oct.	8 Sept.	3 Nov.	56
Heppner	94	9 Oct. ±1.2	8 Oct.	17 Sept.	1 Nov.	45
Northeastern Oregon Total:	744	2 Oct. ±0.4	1 Oct.	4 Sept.	3 Nov.	60
South Cascades	90	1 Oct. ±1.5	29 Sept.	29 Aug.	7 Nov.	70
Coast Range	50	28 Sept. ±1.6	25 Sept.	7 Sept.	24 Oct.	47
Western Oregon Total:	140	30 Sept. ±1.1	28 Sept.	29 Aug.	7 Nov.	70
Vancouver Island Total:	76	28 Sept. ±1.6	24 Sept.	10 Sept.	30 Nov.	81

[1]Standard error in days.
[2]50% of the conceptions occurred before and after this date, respectively.
[3]Number of days between earliest and latest conception dates.
[4]Includes 20 conception dates from elk collected in the Minam Unit, 1983 and 1984.

Table 26. Spring calf:cow ratios for the Grilse and Greenstone herds

Year	Herd	No. classified	Adult bulls[1]	Yearling bulls	Cows	Calves	Calves per 100 cows	% Calf loss from previous summer count[2]	% Calf loss from previous summer count including natural cow mortality[3]	% Calf loss from previous summer count including natural cow mortality and harvest[4]
1982	Grilse	148		8	107	33	31	52	55	58
	Greenstone	78	4	4	53	17	32	—	—	—
1983	Grilse	110		8	73	29	40	18	24	28
	Greenstone	88	13	2	51	22	43	12	18	22
1984	Grilse	79	3	3	58	15	26	30	35	38
	Greenstone	49	8	2	27	12	44	20	25	30
1985	Grilse	93		4	55	33	45	0	6	12
	Greenstone	82	1	8	51	23	60	—	—	—
1986	Grilse	129	4	8	85	32	38	11	16	22
	Greenstone	33	2		21	10	48	20	26	30

[1]Counts of adult bulls are unrealistically low because of the bias for locating cow/calf groups containing radio-collared cows and the more solitary nature of adult bulls.

[2]Assuming 100% cow survival, 1982 values were estimated even though counts of a sufficient sample size were not made during the summer of 1981 (see Section 3.6.1). These are for illustrative purposes only since the winter of 1981/82 had the most severe weather conditions experienced during the study (see Section 4.2.2.2).

[3]6% natural cow mortality based on the mortality rates of radio-collared cow elk (see Section 4.6.3).

[4]12% cow mortality rate including harvest.

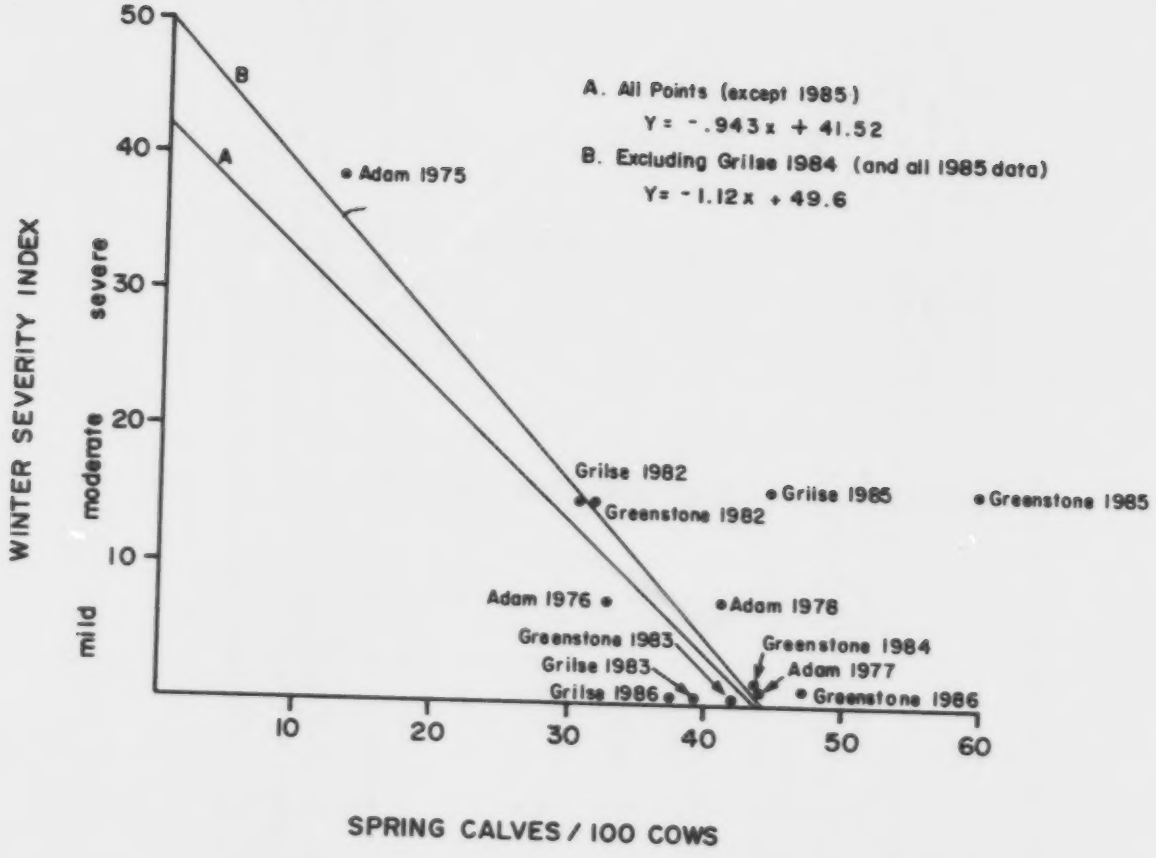

Figure 14. Relationship between spring calf:cow ratios and winter severity. Additional data from Janz (1983).

per 100 cows for 1985 were 45 and 60 for the Grilse and Greenstone herds, respectively, as compared to the values of 31 and 32 obtained for spring 1982. No significant relationship ($.20<p<.50$) was noted between spring calf:cow ratios and winter severity when data from the winter of 1984/85 was added to the analysis.

No winter monitoring occurred during 1985/86 because of the mild weather conditions similar to the winter of 1982/83. Linear regressions were run with 1986 spring calf:cow ratios added to the initial database, using the same severity index as the mild winter of 1982/83. Values from the 1984/85 winter and spring 1985 calf:cow ratios were excluded because of the previous insignificant results when these values were added to the database. Even with the additional data from 1986, winter severity significantly correlated with spring calf:cow ratios, including the 1984 Grilse herd values ($p<.0001$; $r^2=.689$) and excluding them ($p<.005$; $r^2=.89$) (Figure 14).

These results indicate that although there appears to be a relationship between spring calf:cow ratios and previous winter severity, more data from moderate to severe winters are needed to clarify this relationship. Data obtained from the moderate winter of 1984/85 did not follow the pattern of earlier years. The winter of 1984/85 may have been more appropriately labelled a mild winter because of the number of snow melt periods that occurred between snow accumulation periods. Elk in the study area may have experienced little or no stress; however, comparing diet composition between the winters of 1981/82 and 1984/85 (both classified as moderate) shows little difference. Diet composition between moderate and mild winters were distinctly different (see Section 4.7.4.2). Other factors, such as predation, which may not be directly related to snow accumulations, may also have affected calf survival over the winter period.

Calf survival over the winter (August to April) ranges from 62 to 88% during the three mild winters (1982/83, 1983/84, 1985/86) and the one moderate winter (1984/85) (Table 27). Values estimated for calf survival from 1981 to 1982 were listed for illustrative purposes only. Counts were of an insufficient sample size to estimate calf survival within 80% confidence limits. Survival of calves from birth (May and June) to August was not estimated though it is during the first 3 months that high mortality, particularly from predation, can occur. If the estimated pregnancy rate (85.5%) is used to calculate calf production, there could potentially be 30-57% calf mortality occurring by August and an annual survival rate of calves ranging from 26 to 49%. These estimates for calf mortality are high because it is difficult to distinguish between yearling cows (not yet producing calves) and adult cows, thus confounding the calves per 100 cow ratios. Adjusting for this bias (of about 10%, see Section 4.6.6) results in a lower calf mortality rate of 22-51% by August and an annual survival rate of 30-54%.

Table 27. Calf survival (August to April) for the Grilse and Greenstone herds

Herd	Preceding summer calves: 100 cows	Following spring calves: 100 cows	Calf survival assuming 100% cow survival	Calf survival assuming 6% natural mortality of cows	Calf survival assuming 12% natural and harvest[1] mortality of cows
Grilse[2]	65 (1981)	31 (1982)	.47	.45	.42
Grilse	49 (1982)	40 (1983)	.82	.77	.72
Greenstone	49	43	.87	.82	.76
Grilse	37 (1983)	26 (1984)	.70	.66	.62
Greenstone	55	44	.80	.75	.70
Grilse	45 (1984)	45 (1985)	100	.94	.88
Greenstone	46	60	—	—	—
Grilse	43 (1985)	38 (1986)	.87	.82	.62
Greenstone	60	48	.79	.74	.69

[1]Based on estimated mortality rates of radio-collared cow elk (see Section 4.6.3)

[2]Counts of a sufficient sample size (n=94 [from Section 3.6.1] as compared to the actual sample counted n=66) were not obtained during the summer of 1981. Results are presented for illustrative purposes only.

4.6.3 Mortality rates of study animals

An annual estimated mortality rate of 11.7% for yearling and older cow elk in the study area was calculated using a method similar to that outlined by Gasaway *et al.* (1983) from mortalities of radio-collared elk and Limited Entry Hunt (L.E.H.) success rates during the study period (Table 1). This estimate includes predation (3.6%), legal hunting (5.7%), and poaching (2.4%) (Table 28). Radio-collared calves were not included in the analysis. Survival rates of calves were estimated from aerial surveys and are reported in Section 4.6.1, "Calf production". Elk No. 332 was also not included in the estimate as she was shot legally by a hunter who did not see the radio-collar. (All L.E.H. elk hunters were requested by mail to avoid shooting radio-collared elk, so this mortality was considered extraordinary and excluded from the analyses). The estimated poaching loss of 2.4% is probably well below actual levels because an illegal hunter would likely select a non-radio-collared elk to avoid detection. Also, one other adult female (No. 311) could not be detected 7 months after radio-collaring. Although collar malfunction or emigration are possible explanations, poaching is considered a more likely explanation for the disappearance.

Actual mortality rates from illegal hunting and natural causes may also be higher than those reported here because eight radio-collared females were not located as of May 1986, but for the analyses were assumed to be alive. (They were alive early in 1985, but the transmitter batteries on their collars may have worn out). If some or all of these radio-collared elk did die as of May 1986, the minimum estimated mortality rates presented here would increase.

Estimated mortality rates for adult male elk in the study area were much higher than those for females, although sample size of radio-collared males was very low (n=7). An annual estimated mortality rate of 87.6% (33.6% L.E.H. kill; 54.0% poaching and natural mortality) was calculated (Table 29). These values are likely an overestimate because the population level of bulls was developed from ratios obtained in classification flights. An estimated 20 yearling and older bulls:100 cows was used from classification flights of the Grilse and Greenstone herds from 1982 through 1984. However, because bulls generally remain alone or in small groups apart from the larger cow/calf groups (which were primarily sought during classification flights), they are more difficult to observe, and therefore 20 bulls:100 cows is probably an underestimate of the ratio of bulls in the population. This would result in actual mortality rates for bulls being significantly less than the estimates reported here.

Mortality rates of subadult (<3 years old) bulls may be high as a result of aggressive encounters with fully mature bulls. Two 2.2-year-old bulls, which had been radio-collared 5 months earlier, were found dead in August. Both times, the exact cause of death could not be determined, but the time of

Table 28. Mortality rates of radio-collared[1] adult female elk

Animal identifier	Length of time collared (months)	Status as of May 86	Age as of May/86 death, or collar drop (yr)
222	63	Assumed alive	8.0
61	58	Transplanted 01/86	9.0
490	51	Assumed alive	8.0
391	48	Dropped collar	8.0
262[2]	59	Poached 02/86	10.0
22[2]	3	Wolf kill 06/81	4.0
311	7	Disappeared 10/81	4.5
271	61	Known alive	9.0
540	42	Assumed alive	7.0
1085	26	Known alive	6.0
342[2]	20	Wolf kill	8.5
432	62	Assumed alive	12.0
641	50	Known alive	13.0
42	62	Assumed alive	14.0
1014	62	Known alive	16.0
631	50	Known alive	16.0
561	49	Assumed alive	17.0
252[2]	approx. 60	Mortality approx. 03/86	20.0
1037	62	Assumed alive	20.0
591	50	Assumed alive	19.0
1280[2]	17	Poached 01/85	13.5
601	20	Known alive	7.0
551	20	Known alive	6.0

23 elk total 1002 collar months

Mean collaring interval = 1002 months/23 elk = 43.6 months

Mortality Rates

Poaching - 2/23 = 8.7%/43.6 months = 0.2%/mo = 2.4%/yr
Natural Causes - 3/23 = 13.0%/43.6 months = 0.3%/mo = 3.6%/yr
(L.E.H. antlerless kill - 1981-1984 = 73 elk/4 yr = 18.3/yr
18.3 elk/320 est. total antlerless pop. = 5.7%/yr)

[1]Elk No. 332 excluded from analysis because of accidental kill during legal hunting season.
[2]Known mortalities during the study.

Table 29. Mortality rates of radio-collared male elk

Animal identifier	Length of time collared (months)	Status as of May 86	Age as of May/86 death, or collar drop (yr)
241[1]	5	Natural mortality 08/81	2.2
410[1]	5	Natural mortality 08/81	2.2
291	approx. 24	Dropped collar 1983	4.8
371	4	Dropped collar 07/81	3.1
611[1]	7	Poached 02/82	3.7
621	14	Disappeared 05/83	4.0
1140	7	Dropped collar 10/81	11.5
	7 elk total	66 collar months	

Mean collaring interval = 66 months/7 elk = 9.4 months

Mortality rates:

Poaching - 1/7 = 14.3%/9.4 months = 1.5%/mo = 18.0%/yr
Natural Causes - 2/7 = 28.6%/9.4 months = 3.0%/mo = 36.0%/yr
(L.E.H. antlered kill - 1981-1984 = 86/4 yr = 21.5/yr
21.5 elk/64 min. est. total bull pop. = 33.6%/yr)

[1]Known mortalities during the study.

year suggests that malnutrition would not be likely because elk are typically in prime condition at this time of year. A high level of animal condition would also allow adult elk to escape predation relatively easily. Predators would probably be concentrating their hunting activity on deer and calf elk, which are more easily captured. Illegal hunting is a possible cause of death for one of these elk, which was found within 0.5 km of a well-used logging road, but highly unlikely in the other instance where human access, even on foot, was extremely difficult. The radio-collared bull that was found dead in the more remote area was located in a bog adjacent to a recently used wallow - a wet, muddy depression where mature bulls roll, advertising their presence through auditory, visual, and olfactory signals to challenge other bulls. Aggressive encounters to establish dominance and breeding privileges before the actual breeding season (September and October) are probably common among bulls, and it is possible that both of these radio-collared elk died from injuries sustained during fights with other bulls.

4.6.4 Predation

Several sightings of cougars were recorded during the study, but no estimates of cougar densities were made. One adult cougar was observed following a large group of cow and calf elk on the Grilse Creek summer range, but it is unknown if a kill resulted (T. Sterling, pers. comm., July 1981). Janz and Hatter (1986) noted that previous studies indicate cougar predation is not a significant mortality factor of deer on Vancouver Island.

Black bear predation on elk calves has been noted where bears have apparently learned to hunt ungulate neonates selectively (Schlegel 1976). Hatter (1983) noted only minor use of deer fawns and no use of elk calves in bear scat analyses from the Adam River on Vancouver Island. Four adult bears were seen to approach within 200 m of an elk calving site on the Grilse Creek summer range, and although the cow elk appeared to be nervous, the bears were apparently feeding on vegetation and not actively seeking elk calves. Quantitative assessments of bear predation influences could be obtained from scat analysis, but bear predation is not considered an important mortality factor of elk. Both wolves and bears apparently scavenge off dead elk, as a single wolf and bear were seen at the site of a capture mortality several days after death.

Analysis of wolf scats collected April through August 1981 indicated that elk comprised 57.7% (11.0% calves, 46.7% adults) of the wolves' summer diet on a relative weight basis (Becker 1982) (Figure 15). Based on an assumed minimum food intake requirement of 1.7 kg food per wolf per day (Mech 1977), one wolf would have consumed 0.8 calves and 0.5 adults over the summer period (Table 30).

From home range information collected on Vancouver Island wolves (Hatter 1983) it is probable that two separate wolf packs occupy the Grilse and

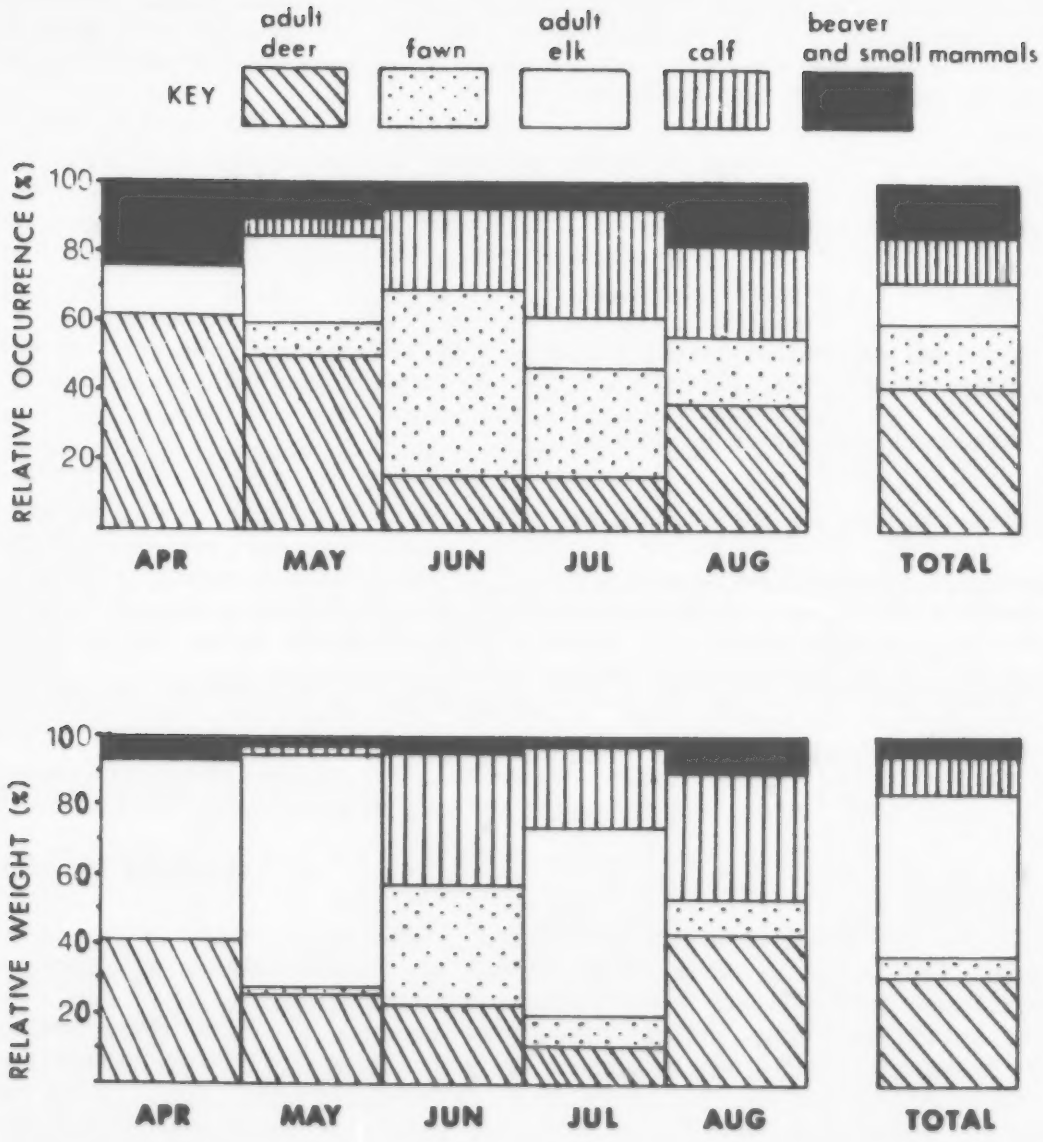

Figure 15. Contents of wolf scats (n=95) collected along logging roads, represented as both frequency of occurrence (%) and relative weights (%) (from Becker 1982).

Table 30. Estimated number of elk calves and adults consumed per wolf between April and August 1981, based on mean weight consumed per scat (adapted from Becker 1982)

Variable	Calves	Adults
Estimated mean weight (kg) consumed per scat[1]	1.3	6.0
Frequency of occurrence (%)	13.4	12.2
Relative weight (kg)	14.1	59.5
Relative % of total biomass consumed	11.0	46.7
Estimated weight (kg) of prey consumed in summer for one wolf (153 days)	28.6	121.4
Estimated mean consumable weight (kg) of individual prey[3]	36.0	222.8
Number of individuals eaten per wolf	0.8	0.5
Number of individuals eaten per pack[4]	4.6	2.9

[1]From Floyd *et al.* (1978) equation, $Y = 0.38 + 0.02x$.
[2]Assuming 1.7 kg food/wolf per day.
[3]Calculated at 0.80 x total weight for elk calves and adults (Fuller and Keith 1980).
[4]Based on an average pack size in summer of 5.8 wolves (Hatter 1983).

Greenstone summer ranges. Based on an average pack size of 5.8 wolves during summer (Hatter 1983), wolves would kill an estimated 4.6 calves and 2.9 adult elk during the April-August period (Table 30) on both the Grilse and Greenstone summer ranges. This would represent a combined calf and adult mortality rate of 4.7% for the Grilse herd and 6.9% for the Greenstone herd during this period.

Average calf:cow ratios obtained in August for the Grilse herd indicated approximately 50 calves per 100 yearling and older cows. That more calves were estimated to have been taken by wolves over the summer period, in spite of their lower proportion in the population, suggests that wolves are selecting calves over adults, probably because they are more easily captured.

Wolf predation on calf elk is probably most significant during the first weeks of life when the calf is most easily captured. However, adult elk may also be relatively easy prey for wolves. During an aerial (helicopter) population survey in April 1984, two wolves were observed to kill an 11-month-old elk, which initially tried to escape by swimming into a small lake. A larger group of elk were in the vicinity and it appeared that the victim had been separated from the group before the survey crew arrived. Wolf density indices have been shown to be negatively correlated with black-tailed deer juvenile recruitment and population level indices on Vancouver Island and there is concern over the ability of wolves to reduce or eliminate elk herds during severe winters (Janz and Hatter 1986). Elk calf:cow ratios may have declined on northern Vancouver Island in response to increasing wolf densities and declining deer densities (Hebert *et al.* 1982). In the spring of 1986, a wolf control program was initiated on northern Vancouver Island, including the study area, and elk population monitoring will continue to assess the impact of the control program.

4.6.5 Age structure

Pooled age estimates from tooth samples of radio-collared elk (n=30) and harvested elk (n=96), including harvest data from 1977 to 1984, provided female age structure data for the study area. The combined age structure from the study area and adjacent watersheds for the same time period (n=206) are illustrated in Figure 16. The age structure for the male segment of the population from the study area and combined areas (n=135 and 303, respectively) are shown in Figure 17. The first three age classes are underestimated in these samples because (1) they have been sampled less than 3 years, and (2) there was a capture and hunting bias for adults and larger animals. The influence of a severe winter in 1970/71 can be seen by the decreased number of elk in the 1971 age class.

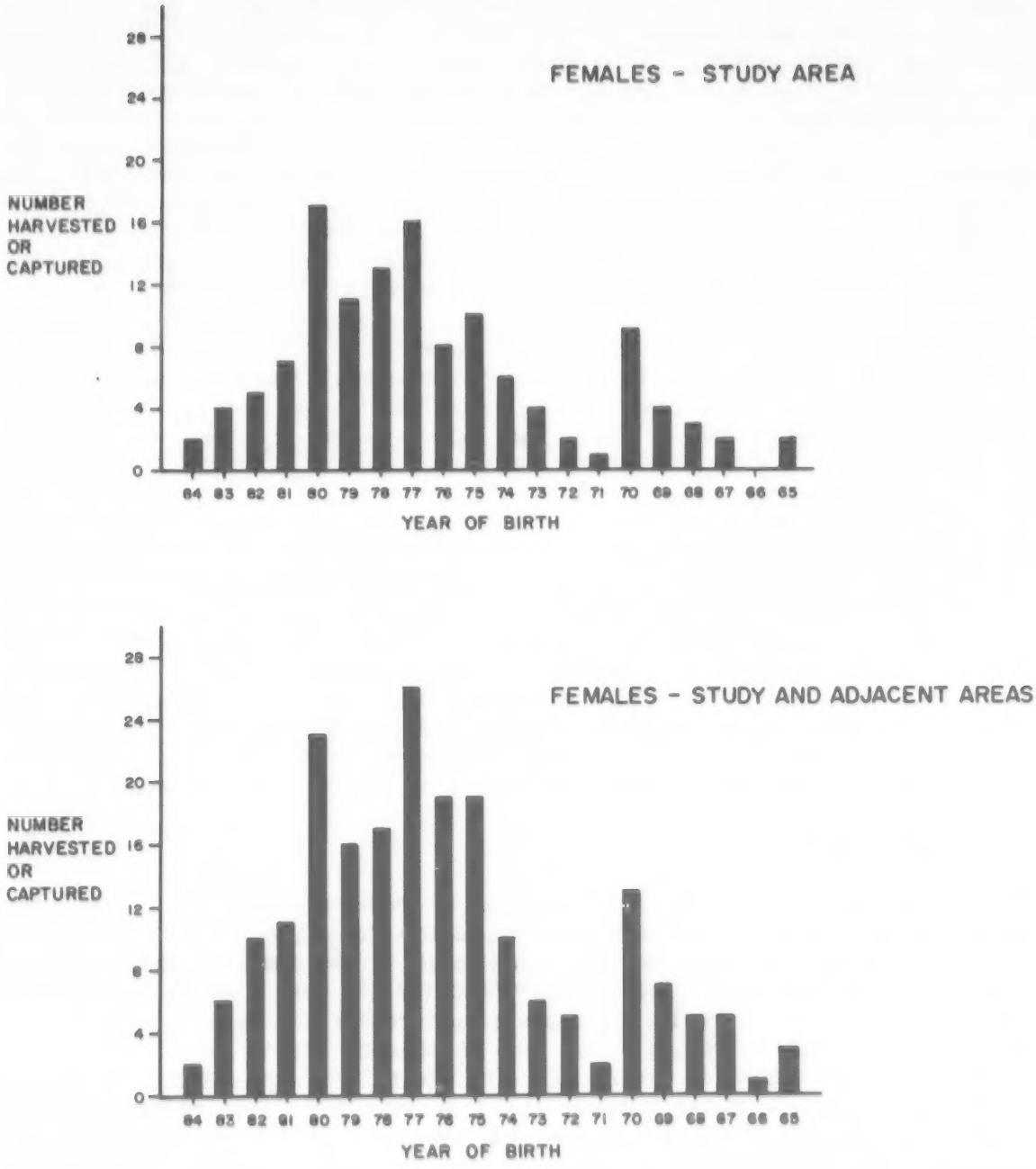

Figure 16. Age structure of females in the study area and adjacent areas from captured and harvested animals.

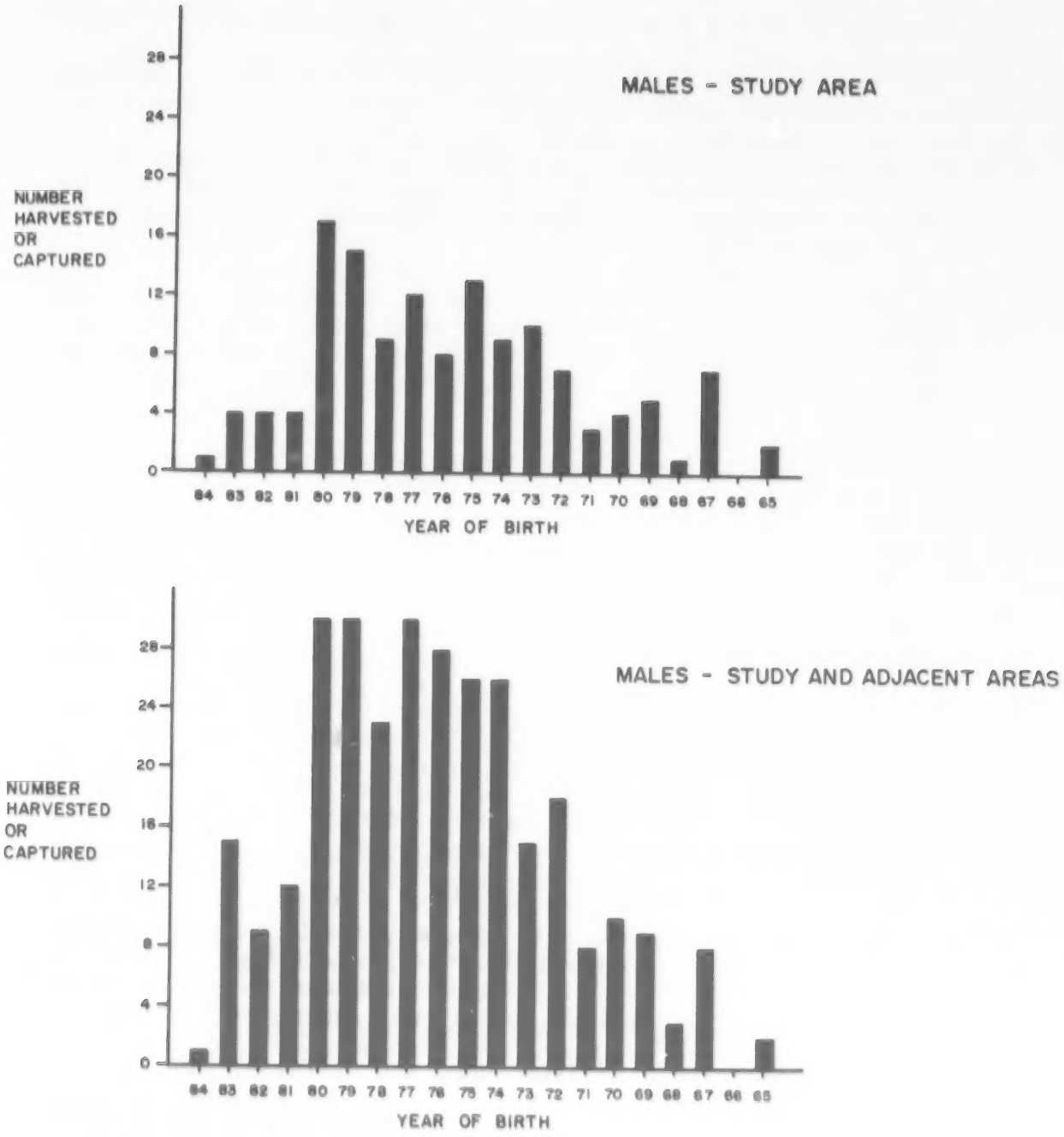

Figure 17. Age structure of males in the study area and adjacent areas from captured and harvested animals.

4.6.6 Life tables

Pooled age estimates from tooth samples of radio-collared elk and harvested elk from the study area were combined (n=261) to calculate life tables for the female and male segments of the population (Tables 31 and 32). The male life tables are biased because of the skewed distribution of ages due to harvest regulations. Generally, life tables are only calculated for the female segment of the populaton; these male life tables were calculated for illustrative purposes only.

A second set of life tables were calculated by incorporating harvest data from adjacent watersheds for the same time period (Tables 33 and 34). Home ranges and migration data indicated that although elk generally show high fidelity to patterns of seasonal range use, there is some interchange between herds of adjacent areas.

Caughley (1977) suggested that at least 150 determinations of age were needed to calculate a life table which would be accurate for any purpose. Adding adjacent watershed data to the study increased female sample size from 126 to 206 age determinations (males increased from 135 to 303). There appeared to be no appreciable differences in proportions in each age class between the study area and combined adjacent areas.

Life tables were calculated by transforming the data and smoothing it, using the log polynomial form of the quadratic equation (Caughley 1966). These adjusted frequencies are seen in column 2 of the life tables (Tables 31-34). If the initial age frequencies had not been adjusted, mortality (d_x) calculations would have turned out to be negative numbers and would be, as Caughley (1977) states, "a biological impossibility". The other columns of the life tables are calculated as per Caughley (1977), with the values in the zero age class being calculated from age-specific fecundity rates (see Section 4.6.1).

Weighted mean mortality rates were also computed for selected age groupings. Mortality rates for juveniles and yearlings are read off the life tables as q_0 and q_1, respectively. Mortality rates are computed for adults in the age classes 2 to 10, over 10 years old, and all adult age classes combined.

Of the different schedules of a life table, the q_x and p_x were the most useful calculations (Figures 18 and 19). The q_x schedule was least affected by sampling bias, gave the most direct projection of the mortality pattern, and could be used for comparative purposes. The p_x schedule can be used in harvesting calculations and population modeling.

Results indicate mortality rates of 6-8% for adult cows from ages 2 to 10, while from ages 10 and older, the mortality rates accelerate to 20%. Yearling cow mortality rates are more variable, ranging between 1 and 6%, while calf mortality reaches between 70 and 75%. When these values were

Table 31. Life table for cow elk in the study area (n=126)

Age Class (x)	Adjusted frequency (F_x)	Survival (l_x)	Mortality (d_x)	Mortality rate (q_x)	Survival rate (p_x)
0	41.2	1.00	.7445	.7445	.2555
1	10.526	.2555	.0031	.012	.988
2	10.3975	.2524	.0061	.024	.976
3	10.1483	.2463	.0087	.035	.965
4	9.7872	.2376	.0112	.047	.953
5	9.3266	.2264	.0132	.058	.942
6	8.7819	.2132	.0149	.070	.930
7	8.1705	.1983	.016	.081	.919
8	7.5113	.1823	.0167	.092	.908
9	6.8231	.1656	.0170	.103	.897
10	6.1241	.1486	.0168	.113	.887
11	5.4314	.1318	.0163	.123	.876
12	4.7596	.1155	.0155	.134	.865
13	4.1213	.100	.0144	.144	.856
14	3.5262	.0856	.0132	.154	.846
15	2.9810	.0724	.012	.166	.834
16	2.4902	.0604	.0105	.174	.82
17	2.0554	.0499			

Column 1 (x): Age (x) at intervals of 1 year.

Column 2 (F_x): Data have been smoothed through the log-polynomial and presented as the number still surviving at 1, 2, 3, etc., years after birth.

Column 3 (l_x): A scaled-down version of column 2 formed by dividing each value by the original strength of the cohort to give the proportion of the cohort still surviving at a given age. Each of these values is designated l_x - the probability at birth of surviving to the exact age x - and termed "survivorship" or simply "survival".

Column 4 (d_x): The probability of dying during the age interval x, x+1. This d_x, the frequency of mortality, calculated as the differences between two consecutive values of l_x.

Column 5 (q_x): The mortality rates q_x, each of which is the proportion of animals alive at age x that die before age x+1. They are calculated as d_x/l_x.

Column 6 (p_x): The survival rates p_x, being the proportion of animals alive at age x that survive to age x+1. They are the complements of their respective q_x values (Caughley 1977).

Weighted mean mortality rates:

Juvenile and yearlings are read as q_0 and q_1, respectively.

Adult cows: Ages 2-10 .0603
Ages 10+ .208
All adult cows: .077

Table 32. Life table for bull elk in the study area (n=135)

Age Class (x)	Frequency (F_x)	Survival (l_x)	Mortality (d_x)	Mortality rate (q_x)	Survival rate (p_x)
0	44.27	1.00	.584	.584	.416
1	18.40	.416	.047	.113	.887
2	16.36	.369	.04	.108	.891
3	14.55	.329	.037	.112	.887
4	12.94	.292	.032	.109	.890
5	11.50	.260	.029	.111	.888
6	10.23	.231	.026	.112	.887
7	9.094	.205	.022	.107	.892
8	8.085	.183	.021	.115	.885
9	7.19	.162	.018	.111	.889
10	6.394	.144	.016	.111	.889
11	5.68	.128	.014	.109	.890
12	5.05	.114	.013	.114	.885
13	4.49	.101	.011	.109	.891
14	3.99	.090	.01	.111	.889
15	3.55	.080	.009	.112	.8875
16	3.16	.071			

Column 1 (x): Age (x) at intervals of 1 year.

Column 2 (F_x): Data have been smoothed through the log-polynomial and presented as the number still surviving at 1, 2, 3, etc., years after birth.

Column 3 (l_x): A scaled-down version of column 2 formed by dividing each value by the original strength of the cohort to give the proportion of the cohort still surviving at a given age. Each of these values is designated l_x - the probability at birth of surviving to the exact age x - and termed "survivorship" or simply "survival".

Column 4 (d_x): The probability of dying during the age interval x, x+1. This d_x, the frequency of mortality, calculated as the differences between two consecutive values of l_x.

Column 5 (q_x): The mortality rates q_x, each of which is the proportion of animals alive at age x that die before age x+1. They are calculated as d_x/l_x.

Column 6 (p_x): The survival rates p_x, being the proportion of animals alive at age x that survive to age x+1. They are the complements of their respective q_x values (Caughley 1977).

Weighted mean mortality rates:

Juvenile and yearling are read as q_0 and q_1, respectively.

Adult bulls:	Ages 2-10	.111
	Ages 10+	.219
	All adult bulls:	.111

Table 33. Life table for cow elk in the study area and adjacent areas (n=206)

Age Class (x)	Frequency (F_x)	Survival (l_x)	Mortality (d_x)	Mortality rate (q_x)	Survival rate (p_x)
0	74.1	1.00	.6955	.6955	.3045
1	22.5748	.3045	.0181	.0594	.941
2	21.2347	.2864	.0186	.0649	.935
3	19.8550	.2678	.0189	.0706	.929
4	18.451	.2489	.0189	.0759	.924
5	17.0497	.2300	.0188	.0817	.918
6	15.6581	.2112	.0184	.071	.913
7	14.2943	.1928	.0178	.0923	.908
8	12.9714	.1750	.0172	.0983	.902
9	11.7006	.1578	.0163	.1033	.8967
10	10.49	.1415	.0154	.1088	.8912
11	9.35	.1261	.0144	.114	.886
12	8.2848	.1117	.0133	.119	.881
13	7.2963	.0984	.0122	.124	.876
14	6.3874	.0862	.0112	.130	.87
15	5.5584	.0750	.0101	.1347	.8653
16	4.8081	.0649	.0091	.1402	.860
17	4.1342	.0558			

Column 1 (x): Age (x) at intervals of 1 year.

Column 2 (F_x): Data have been smoothed through the log-polynomial and presented as the number still surviving at 1, 2, 3, etc., years after birth.

Column 3 (l_x): A scaled-down version of column 2 formed by dividing each value by the original strength of the cohort to give the proportion of the cohort still surviving at a given age. Each of these values is designated l_x - the probability at birth of surviving to the exact age x - and termed "survivorship" or simply "survival".

Column 4 (d_x): The probability of dying during the age interval x, x+1. This d_x, the frequency of mortality, calculated as the differences between two consecutive values of l_x.

Column 5 (q_x): The mortality rates q_x, each of which is the proportion of animals alive at age x that die before age x+1. They are calculated as d_x/l_x.

Column 6 (p_x): The survival rates p_x, being the proportion of animals alive at age x that survive to age x+1. They are the complements of their respective q_x values (Caughley 1977).

Weighted mean mortality rates:

Juvenile and yearling are read as q_0 and q_1, respectively.

Adult cows:	Ages 2-10	.082
	Ages 10+	.201
	All adult cows:	.093

Table 34. Life table for bull elk in the study and adjacent areas (n=303)

Age Class (x)	Frequency (F_x)	Survival (l_x)	Mortality (d_x)	Mortality rate (q_x)	Survival rate (p_x)
0	111.512	1.00	.61	.61	
1	43.46	.390	.043	.110	.89
2	38.68	.347	.038	.109	.89
3	34.43	.309	.045	.145	.854
4	29.45	.264	.019	.072	.93
5	27.28	.245	.027	.110	.89
6	24.29	.218	.024	.110	.89
7	21.62	.194	.021	.108	.89
8	19.244	.173	.019	.109	.89
9	17.13	.154	.017	.110	.89
10	15.25	.137	.015	.109	.89
11	13.57	.122	.014	.115	.885
12	12.08	.108	.012	.111	.888
13	10.75	.096	.01	.104	.89
14	9.57	.086	.01	.116	.884
15	8.52	.076	.008	.105	.894
16	7.58	.068			

Column 1 (x): Age (x) at intervals of 1 year.

Column 2 (F_x): Data have been smoothed through the log-polynomial and presented as the number still surviving at 1, 2, 3, etc., years after birth.

Column 3 (l_x): A scaled-down version of column 2 formed by dividing each value by the original strength of the cohort to give the proportion of the cohort still surviving at a given age. Each of these values is designated l_x - the probability at birth of surviving to the exact age x - and termed "survivorship" or simply "survival".

Column 4 (d_x): The probability of dying during the age interval x, x+1. This d_x, the frequency of mortality, calculated as the differences between two consecutive values of l_x.

Column 5 (q_x): The mortality rates q_x, each of which is the proportion of animals alive at age x that die before age x+1. They are calculated as d_x/l_x.

Column 6 (p_x): The survival rates p_x, being the proportion of animals alive at age x that survive to age x+1. They are the complements of their respective q_x values (Caughley 1977).

Weighted mean mortality rates:

Juveniles and yearlings can be read as q_0 and q_1, respectively.

Adult bulls:	Ages 2-10	.110
	Ages 10+	.219
	All adult bulls:	.110

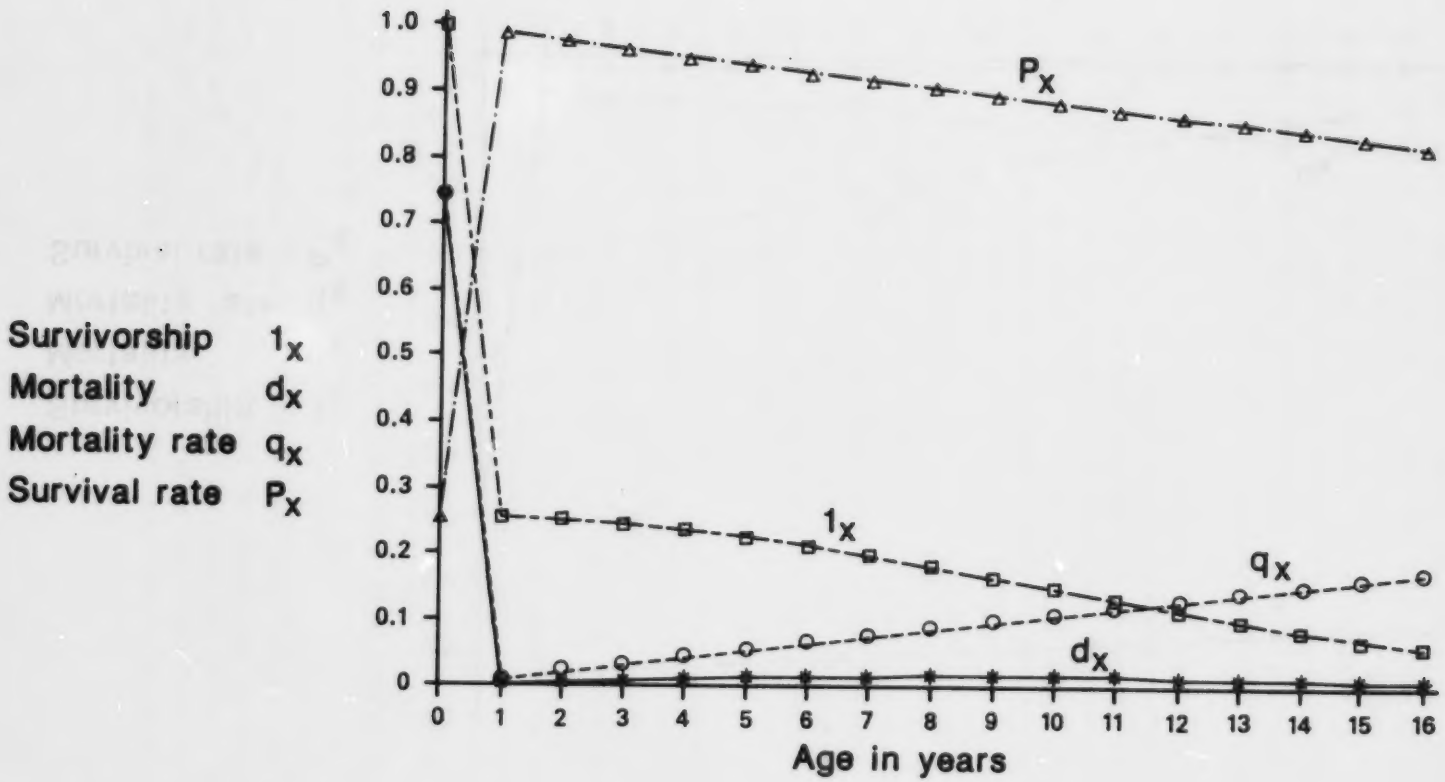

Figure 18. Representation of life table schedules of female Roosevelt elk from the study area (refer to Table 31).

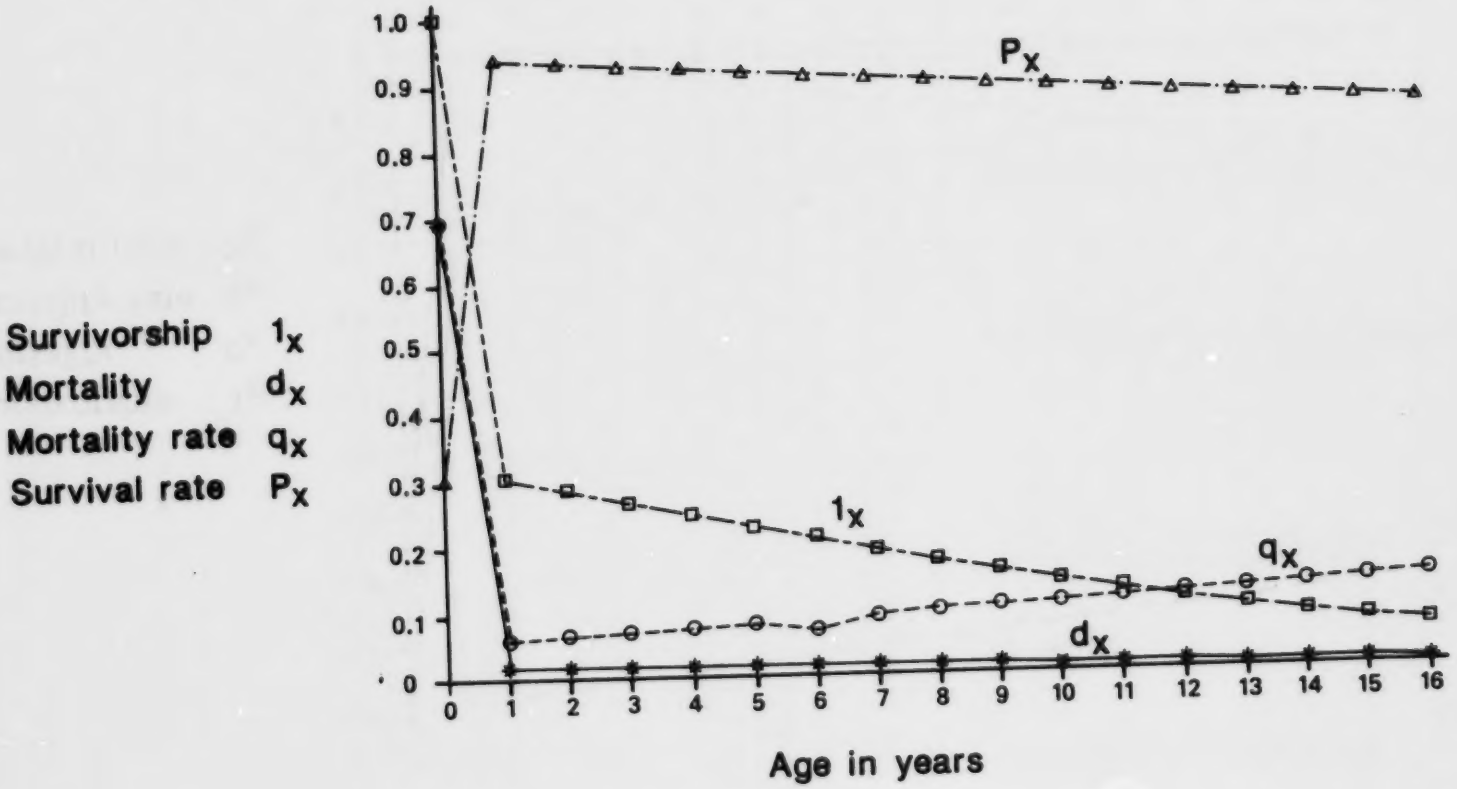

Figure 19. Representation of four life table schedules of female Roosevelt elk from the study area and adjacent areas (refer to Table 34).

compared with estimated calf survival rates (Section 4.6.2), the results from the life table analyses appear to indicate lower survival rates. Annual survival rates estimated from aerial surveys are between 30 and 54% while life tables indicate a survival rate of 25-30%. In comparison, adult cow survival rates calculated from life tables were only slightly higher than those estimated for adult mortalities. Adult cow survival rates from life tables were calculated to be from 92 to 94% for adult cows between 2 and 10 years old, and 80% for adult cows over 10 years old. Overall survival rates for all ages of adult cows from life tables were between 91 and 92%. In comparison, estimated adult cow survival rates from radio-collared elk were around 88% for all ages (including yearling cows). Yearling cow mortality was not included with adult cow mortality calculations in life table analyses.

The major difficulty in the analysis of population dynamics of any wild mammal lies in obtaining useful estimates of survivorship (Eberhardt 1985). The general pattern of mortality in mammals appears to be age-dependent, with a high rate in the youngest age classes, a low rate in middle age classes, and a marked senescence in older age classes (de la Mare 1985). Often, different procedures are used to estimate early survival, survival over prime age-classes, and survival in senescence. Because survivorship of the prime age-class animals has the major impact on population growth, the best estimates should be researched there (Eberhardt 1985). Bias can be high in estimating early survival, and early survival can have less impact on the estimated growth rate than adult survivorship. Also, fitting the data on senescence does not have as major an impact on populations as adult survivorship (Eberhard 1985). Despite their limitations, both early survival and senescence should still be estimated.

Examining the differences between life table estimates and other estimates may only be critical when there are large discrepancies between estimated survival values for the prime age class animals. This could signal population changes that might have long-term effects on all age classes.

The survival curves (Figures 18 and 19) indicate that mortality occurs most in the early stages of life (Seber 1982), with calf mortality being the major factor that limits the growth of these specific populations. Although there are differences in estimated calf survival between life tables and aerial censuses, both indicate high mortality in that age class. Life tables indicate a lower and less variable survival rate than those estimated from age ratio data collected on aerial surveys.

However, age ratio estimates must be interpreted cautiously. Before they can be interpreted critically, age ratios should be supported by estimates of the rate of increase and of survival or fecundity (Caughley 1977). Age ratios do not reflect the dynamics of a population: when calf survival is high it does not necessarily mean that the remainder of the population is either

increasing or has a high survival rate. Changes in parameters because of density dependence may influence age structure and, therefore, age ratios. Even though age ratios may reflect the change to a certain extent, the change cannot be calculated from age ratios alone. If calf survival suddenly drops or increases, the effects on the population should be examined using other trend data (e.g. population age structure, rates of increase, and mortalities of prime age class animals).

Attempts were made in this study to incorporate rates of increase into life table computations. Theoretically, life tables are built upon stable, stationary populations. A population is said to be stable when the birth and mortality rates are constant over time and the age distribution eventually assumes a stable form (Seber 1982). The population is said to be stationary when the population remains constant in size. The rate of increase, r, is zero and the size of each age class remains constant (Seber 1982). All stationary age distributions are stable, but only some stable age distributions are stationary (Caughley 1977). Because life tables can be calculated from populations that are stable but not necessarily stationary, rates of increase should be incorporated into data before life table analyses are conducted (Caughley 1977).

The intrinsic rate of increase, r_m, is the maximum rate at which a population with a stable age distribution can increase when no resource is limiting. It is determined by the climate, quality of food, shelter, and other environmental influences interacting with an animal's genetically determined capacity to reproduce and survive (Caughley and Birch 1971). The intrinsic rate of increase is required to estimate how fast a population will grow after being reduced to a minimal density, and to estimate a sustained yield harvest. Assuming there was a stable age distribution in this study's data (the composition of the age structure data appeared to be relatively constant during each year), rates of increase should have been incorporated.

The intrinsic rate of increase was calculated using Lotka's (1907) equation:

$$\Sigma \; l_x e^{-rx} m_x = 1$$

where l_x = survivorship
m_x = fertility
r = innate capacity for increase
x = age class

For the female segment of the population, the estimate was between .088 (study area) and .084 (study area plus adjacent watersheds). The observed rate of increase from population censuses (Section 4.6.7) was approximately .10 (10%), thus the estimates for the intrinsic rate of increase do not seem unreasonable. However, Tait and Bunnell (1980) point out that, although it

is possible to estimate r in theory, it is virtually impossible to estimate in practice. Bias results from using survival (l_x) values from a sample of dead animals, and even though the bias can be reduced, confidence intervals placed on r from finite populations show that unacceptable values of r are obtained. The situation worsens in finite populations that have very small changes from year to year in survivorship and fecundity.

Incorporating values of r into the data (whether it was estimated from population counts or as r) did not improve the fit of the data to the log-polynomial form of the quadratic equation (used for smoothing the data before it was incorporated into life table analyses). Although there is population growth occurring in the study area, it is difficult to assess and incorporate it into life tables at this point.

Eberhardt (1985) pointed out the importance of using population trend data in conjunction with age structure and reproductive data, and of using population modeling in evaluating possible management scenarios. As previously mentioned, the problem of biases in estimating adult survivorship is critical because only a few percentage points of adult survival separate increasing and decreasing populations. Therefore, incorporating reasonably accurate life table estimates with population and fecundity data is very important. Further research and data collecton are required before population dynamics can be summarized with the aid of functional models of survivorship and reproduction. Ultimately, population modeling may be able to determine whether habitat management techniques are providing enough correct habitat variables for a population to grow at a rate that will sustain a harvest of certain age classes and remain a healthy, viable population.

4.6.7 Population estimates

Population density (Table 35) varied by herd and season. The migratory herds (Grilse and Greenstone) had the highest summer densities of 3.6-6.5 elk per km^2. Winter densities were similar on most ranges with approximately 3.0-4.0 elk per km^2. The winter density estimate for the Lower Salmon herd (1.6 elk per km^2) probably underestimates actual density because a migratory herd (of unknown size) has an overlapping winter range.

Structured aerial surveys were not conducted because of the nature of the study and the intensive methods required in forested habitats for extensive population surveys. Productivity (August surveys) and over-winter calf survival (March/April surveys) were assessed based on the ratio of calves per 100 cows (Section 3.6.1).

Table 36 shows estimates of population sizes and trends. Although these estimates are reasonable, the combination of techniques used in estimating population size resulted in large, overlapping confidence intervals that

Table 35. Annual and seasonal herd area and density estimates for four herds in the study area.

		Herd range area (km²)			Herd density (elk/km²)[2]		
Herd	N[1]	Annual	Summer	Winter	Annual	Summer	Winter
Grilse	130	200	20	30	0.6	6.5	4.3
Greenstone	90	150	25	30	0.6	3.6	3.0
Lower Salmon	40	25	25	25	1.6	1.6	1.6[3]
Greybe's	30	10	10	10	3.0	3.0	3.0

[1]1983 population estimates of total number of cows and calves in the herd are based on composite information from Petersen-index calculations (based on ratio of radio-collared elk seen to radio-collared elk present), radio-telemetry, and general knowledge of the herd.
[2]Density estimates are for cow-calf groups, and exclude adult bulls.
[3]Densities may be higher than this during winter, as a migratory herd (of unknown number) shares the same winter range.

Table 36. Population trends between years using summer counts

Year	Herd	n[1]	N[2]
1982	Grilse	109 (102)	120
	Greenstone	58 (73)	80
1983	Grilse	118 (73)	130
	Greenstone	79 (39)	90
1984	Grilse	125 (88)	143
	Greenstone	54 (74)	100
1985[3]	Grilse	83 (117)	158
	Greenstone	68 (31)	110

[1]Sample size of cows and calves counted on summer surveys (bracketed values are the following spring counts).
[2]Population estimate of total number of cows and calves in herd, based on composite information from Petersen estimates, radio-telemetry, and general knowledge of the herd.
[3]Population counts were slightly lower because of lack of sampling time.

were not statistically valid. Thus, the estimates were not included in this table. Population modeling is required for a more accurate assessment of future population size and composition. An estimate of a 10% growth rate is probably realistic, based on the available data; a more qualified measure of this rate is required to determine if populations are responding negatively or positively to habitat changes.

4.7 Habitat Use

4.7.1 Spaced stand use

Most spacing within the study area was classified as backlog spacing. These are stands spaced at 20-40 years of age without removal of the resulting debris. Debris from these activities, including tree branches and stems up to 30 cm in diameter, exceeded 2 m in depth in certain areas. Large portions of the Sayward Provincial Forest were backlog spaced during the late 1970's, including much of the Greenstone herd winter range. There was extremely limited juvenile spacing of stands in the 12- to 17-year age category on the Greenstone winter range.

Elk home ranges on the Greenstone winter range were generally located between large backlog spaced areas. Where home ranges included spaced stands, they were significantly avoided ($p<.20$).

Throughout the study, circumstances surrounding observed use of backlog spaced stands were recorded. In most instances, use was restricted to roads or trails running through the stand, or other portions of the stand where debris was minimal. Elk were seen to enter spaced stands with substantial debris only when harassed by a helicopter or humans on foot. After entering the stand, they appeared extremely hesitant to move further into it. Flight distance seemed much less than in stands with similar visibility but no debris. The need for escape cover from wolves was a possible explanation for one instance of observed use of backlog spacing.

The increased energetic expense of travel through the debris of backlog spaced stands is probably the major deterrent to elk use of these areas. An adult female elk which must travel over 0.8 m high (brisket height) obstacles which occur at a frequency of 50 every 100 m expends approximately 14 times more energy than in locomotion without debris (Parker 1983).

There also appears to be an increased danger of injury to elk travelling through spacing debris. The capture mortality which occurred during immobilization of an adult female in this study took place when she fled into a backlog spaced stand and suffered a broken neck. In addition to restricting access to a stand, debris from spacing activities reduces the amount of space available for elk forage species to grow.

Deterioration rates of spacing debris are currently unknown, but are probably dependent on tree species, age (size of trees) at spacing, and pre- and post-spaced densities. Compaction of debris by snowpacks would also influence deterioration rates. Debris in backlog spaced stands that were treated 10 years earlier show signs of decay, but maintain significant debris depths. Directional falling to avoid crossing of trees, and debris treament in the form of bucking, extensive trailing, or complete removal would likely reduce the impact of backlog spacing debris on elk use of a stand. Without debris treatment, it is unlikely that elk would benefit from increased forage as a result of a reduction in canopy closure following backlog spacing activities. Spacing debris, which reduces access to the stand and the amount of space available for the growth of forage plants, may persist until canopy closure once again increases to its pre-spaced level.

4.7.2 Calving habitat use

Calving sites (n=11) were found to occur on the winter range, transitional range, and summer range, although most calving activity occurred on the summer range. Eight of 11 calving sites occurred in second growth (Table 37). Generally, calving sites were located on flat or gently sloping ground among steeper terrain upslope from valley bottoms.

During the calving period, all observed cows were solitary, and remained solitary for a 5- to 20-day period before joining other elk. This period of seclusion apparently allows the newborn calf time to gain strength and become mobile enough to escape predators later when the elk congregate in large, highly visible groups. Two calves captured by hand were associated only with their mother and were noticeably less agile than calves observed in nursery band groups of cows and their offspring. While associated only with their mothers, calves were seen to freeze into immobility, but this hiding strategy was no longer used by the time mothers and calves assembled into groups. During the period of seclusion following calving, both the cow and calf generally used an area of less than 1 ha.

Security appears to be an important criterion in the selection of calving sites. Small, flat areas among steeper terrain offer excellent visibility for predator detection as well as flat ground for the newborn calf to move about easily. All identified calving sites had vegetative cover which readily concealed both the cow and calf and the presence of such cover appears to be an important aspect in the selection of a calving site.

Repeated use of a calving site in consecutive years by individual cows was not observed, although sample size was very small. However, the general area where calving takes place may be repeatedly used. One adult cow returned to a calving site used in the previous year where her calf had been captured for this study. She travelled several kilometres over the subsequent 24-hour period before selecting another calving site. It is suspected that she chose

Table 37. Characteristics of identified calving sites

	ANIMAL IDENTIFIER										
	1982		1983			1984					
	252	Uncollared	41	252	1037	41	262	391	540	1037	1280
Elevation (m)	600	500	700	500	650	250	<50	600	400	600	250
Stand type[1]	6/3[2]	3/6	3	1	3	4/1	2	3	3/1	6/1	4/1
Slope (degrees)	0-20	0	0	0	6	0	0	0-10	0	0-10	0
Overstory height (m)	>30	2	<2	2	<2	10-20	10-20	5	3-5	>30	20-30
Overstory age (yr)	250+	14	7	n/a	3	21-40	21-40	18	12-16	250+	38
Sighting index[3] (m)	---	---	55	50	65	---	---	---	---	---	---

[1]Stand types:
1 = Non-productive forest lands (bogs and rock outcrops)
2 = Deciduous/conifer complex
3 = 1- to 20-year-old conifer
4 = 21- to 60-year-old conifer
5 = 21- to 40-year-old spaced conifer
6 = Old-growth conifer

[2]The first number identifies the most probable stand type where calving occurred; the second indicates an adjacent stand or secondary possible calving site.

[3]The mean distance at which a sighting tube (60 cm diameter; 175 cm height) is hidden from view.

an alternative site either because she was disturbed while being radio-located, or because she lost a calf in the previous year at the original calving site.

A concurrent study of the effects of logging activity on elk calving site selection in the Grilse Creek area in 1986 was unable to positively identify any calving sites. However, from visual observations it appeared that at least two cows may have calved near an active logging truck haul route on the same hillside as other logging activity (blasting and loading).[2] A 400-m wide strip of old-growth forest and topographical barriers prevented line-of-site contact with blasting and loading activity. Topographical barriers may also have separated the actual calving sites from the haul route. The effect of adjacent logging activity on the selection of calving sites by the cow, and on the cow and calf, remain unclear.

4.7.3 Summer habitat use

Summer range habitat use:availability was examined for two intensive monitoring sessions on the Grilse Creek summer range in 1982 and 1983 (Table 38) and throughout the entire summer of 1981 for the Grilse and Greenstone Creek summer ranges (Table 39). Grilse summer range locations obtained during intensive monitoring sessions (1982 and 1983) were taken during both daylight and darkness, while those analysed for the entire summer (1981) were primarily daylight locations. However, patterns of habitat preference were similar. Selection indices were not employed because elk use of habitats was not significantly different from availability.

Percent use of meadow/bog and mixed conifer/deciduous stand types was greater than percent availability on the Grilse summer range, while use of clearcuts in the 6- to 20- and 0- to 20-year-old age classes was approximately equal to availability. However, use of 4- to 20-year-old clearcuts on the Greenstone summer range (where the availability of meadow/bog and mixed conifer/deciduous stand types is extremely limited) exceeded availability. From these data, natural foraging areas (meadow/bog and mixed conifer/deciduous) where available appear to be preferred habitats for foraging activities. When these areas are limited in availability, such as on the Greenstone summer range, forestry-created openings (clearcuts) are more heavily used as foraging areas. Use of clearcuts in the 1- to 5-year-old and 0- to 3-year-old age classes are apparently used slightly less than availability, possibly because of debris remaining from logging activities and the relatively low abundance of elk forage species in the first years after clearcutting.

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[2]Houtman, R. 1986. The effects of logging activity on Roosevelt elk calving site selection. MacMillan Bloedel Ltd., Nanaimo, B.C. Unpublished report.

Table 38. Summer range habitat use:availability for two intensive monitoring sessions conducted on the Grilse Creek summer range

Stand Type	June 28 - July 2, 1982 Area % (ha)	June 28 - July 2, 1982 Locations %(n)	May 30-June 9, 1983 Area % (ha)	May 30-June 9, 1983 Locations % (n)	Combined Area % (ha)	Combined Locations % (n)
Meadow/bog	6.9(21.5)	17.8(8)	5.3(12.5)	16.3(7)	6.2(34)	17.0 (15)
Mature and old-growth conifer	35.1(109.2)	15.5(7)	75.5(177.4)	60.5(26)	52.5(286.6)	37.5 (33)
Mixed conifer/ deciduous	4.3(13.4)	17.8(8)	0.9(2.1)	4.6(2)	2.8(15.5)	11.4 (10)
0- to 20-year-old conifer	53.7(167.0)	48.9(22)	18.2(42.8)	18.6(8)	38.4(209.8)	34.1 (30)
Totals (ha, # locations)	311	45	235	43	546	88

Table 39. Summer range habitat use:availability summary for the Grilse Creek and Upper Greenstone Creek summer ranges; May-October 1981

GRILSE CREEK (elk No. 252)

Stand type	Area % (ha)	Locations % (n)
Meadow/bog	2.2 (17.5)	7.1 (2)
Mature & old-growth conifer	47.8 (381.7)	25.0 (7)
Mixed conifer/deciduous	4.2 (33.5)	25.0 (7)
1- to 5-year-old conifer	12.1 (96.8)	10.7 (3)
6- to 20-year-old conifer	32.2 (256.7)	32.1 (9)
65- to 100-year-old conifer	1.4 (11.2)	0 (0)
TOTALS (ha, no. locations)	797.4	28

UPPER GREENSTONE (elk nos. 262 and 311)

Stand type		
Meadow/bog	0.3 (7.0)	2.8 (1)
Mature & old-growth conifer	55.8 (1212.1)	44.4 (16)
0- to 3-year-old conifer	10.4 (226.3)	8.3 (3)
4- to 20-year-old conifer	27.0 (584.1)	41.7 (15)
51- to 60-year-old conifer	6.5 (141.8)	2.8 (1)
TOTALS (ha, no. locations)	2171.4	36

On both the Grilse and Greenstone summer ranges, percent use of mature and old-growth forest was less than availability. However, use of this stand type composed an average of about 36% of summer range locations, suggesting that it is an important component of summer ranges. The current relative abundance of mature and old-growth forest, which averages approximately 52% of the summer home ranges analysed, may account for the lower use:availability ratio observed for this stand type.

Distance-to-edge was estimated from visual observations of elk on the Grilse and Greenstone summer ranges in recent clearcuts (0- to 10-year-old stands) (Figure 20). Ninety-five percent (n=48) of sightings occurred within 200 m of a forest edge and 50% within 40 m. Ony 5% of observations occurred at a distance greater than 200 m from a forest edge with a maximum observed distance-to-edge of approximately 300 m. Availability of openings greater and less than 200 m from a forest edge was assessed on the Grilse Creek summer range (Figure 20). Approximately 40% of the area in openings was greater than 200 m from an edge. Distribution of opening sizes on the Greenstone summer range are similar.

Skovlin (1982) reviewed some studies that have also identified disproportionately heavy use of edges between foraging areas and security cover. Elk requirements for readily available security cover while they forage in openings, and the wide array of forage associated with edges, are the most common explanations of this observed preference for edge. Typically, areas close to edges between plant communities or successional stages of a plant community possess a greater variety and quantity of elk forage species. At nearly any point within the growing season, some elk forage species are usually in an optimal stage of phenology and stored nutrients near an edge (Skovlin 1982). The heavy use of open summer range foraging areas close to a forest edge is probably a combination of the simultaneous requirement for both forage and adjacent security cover in areas where predator and human activity is relatively high, and the greater forage availability associated with edges.

4.7.3.1 Summer forage selection

Rank comparisons of usage and availability (Johnson 1980) of forage species on the Grilse Creek summer range in 1981 indicate the relative preference of elk for plant taxa during the summer (Table 40). However, a Spearman rank correlation between use and availability was significant ($p<.10$), indicating that use of forage species increased proportionally with availability, and that selection or preference may not have been an important factor in diet composition during summer.

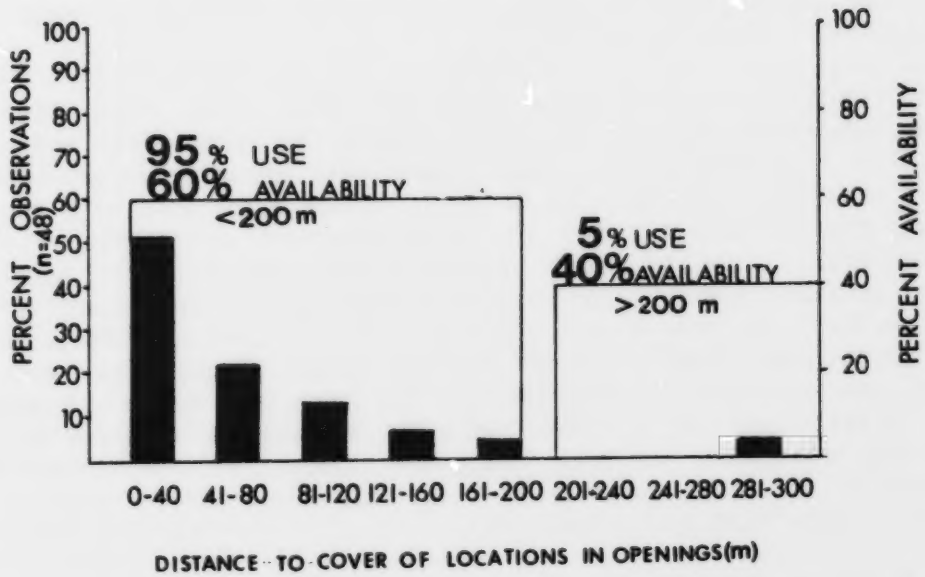

Figure 20. Frequency histogram of the distance to forest edge of elk sighted in 0- to 10-year-old clearcuts, collected from the Grilse and Greenstone herds during summer and fall 1981 and 1982. Availability of openings <200 m and >200 m from a forest edge on the Grilse summer range is also shown.

Table 40. A rank usage-availability comparison between species composition in the summer diet and availability on the Grilse herd summer range, 1981

Forage Class	Species	RANK		Difference	Relative Preference
		Use	Availability		
Conifers	*Tsuga heterophylla*	12.5	7	5.5	15
	Thuja plicata	9.5	24	-14.5	2
	Abies amabilis	5.5	8.5	-3	8
	Pseudotsuga menziesii	19.5	5	14.5	20
Shrubs	*Rubus* spp.	1	6	-5	6
	Cornus canadensis	2	3	-1	9
	Vaccinium spp.	12.5	2	10.5	19
	Myrica gale	19.5	4	15.5	21
	Mahonia nervosa	4	11.5	-7.5	4
	Ledum groenlandicum	19.5	19	.5	11
Forbs	*Achlys triphylla*	19.5	16	3.5	14
	Tiarella trifoliata	19.5	20.5	-1	9
	Streptopus amplexifolius	19.5	22.5	-3	8
	Clintonia uniflora	19.5	18	1.5	12
	Linnaea borealis	9.5	14	-4.5	7
	Mycelis muralis	7	22.5	-15.5	1
	Epilobium angustifolium	8	1	7	17
	Sanguisorba sitchensis	19.5	13	6.5	16
	Anaphalis margaritacea	19.5	17	2.5	13
	Hypochaeris radicata	19.5	10	9.5	18
Ferns	*Polystichum munitum*	14	20.5	-6.5	5
	Blechnum spicant	3	15	-12	3
Grasses		5.5	8.5	-3	8
Sedges		11	11.5	-.5	10

4.7.4 Winter habitat use

4.7.4.1 Habitat selection

Use of habitat types on the winter range (Figure 21) during 1982/83, 1983/84, and 1984/85 was disproportionate to availability, based on relative proportions of radio-locations compared to relative proportions of habitat types available. Availability of habitats was defined by the area encompassed by the minimum area method (Mohr 1947) using all radio-locations obtained during these three winters (Figure 22). Chi-square analysis indicated significant differences between habitats available and habitats used during both mild winters and the moderate winter ($p<.001$). Comparisons in habitat use between the mild winters and the moderate winter indicated that significantly different proportions of habitats were used each year ($p<.001$). Habitat use differed between the two mild winters and between the moderate winter and the mild winters. Use shifted from bogs in mild winters to rock outcrops in the moderate winter, causing some variation between each winter's habitat use. When bogs and rock outcrops (non-productive forest land) were eliminated from the comparisons, the moderate winter of 1984/85 and the mild winter of 1983/84 showed no difference in habitat selection ($.25<p<.50$). However, the mild winter of 1982/83 significantly differed from both the mild winter of 1983/84 ($.25<p<.50$) and the moderate winter of 1984/85 ($.01<p<.25$) in habitat use even with non-productive forest land removed from the analyses.

Selection indices were used to determine habitat preferences, because use was not proportional to availability. If no selection was taking place, habitats would be used in proportion to their availability (See Appendix 1). Although selection may not be an expression of need or preference, it was assumed in this study that selection was a measure of some preference and represented an advantage to elk over the non-preferred alternatives.

Selection for habitat types was determined for each winter home range over a 3-year period for the Greenstone herd. Six radio-collared cows were intensively monitored while on winter ranges from 1982 to 1985 (see Section 3.2.4). Habitat selection was assessed using three indices. The first, a derivation of the chi-square approach, was based on a simple comparison of expected number of locations to the proportion of available area in each habitat type (Table 41). This index, although biased because of unequal availabilities, gives the relative importance of habitat types during each winter. The second index (Table 42) was Strauss' (1979) proposed linear selection model; in brief, t-statistics were used for evaluation and statistical comparison. Although the reliability of the proposed index was dependent upon relative abundances, confidence intervals were smaller for less frequent habitats than for more abundant ones (Strauss 1979). The third index was based on comparing actual use to the proportion of locations that would occur in a habitat if all habitats were of equal abundance (Table 43). Although this did not take into account that the more abundant a habitat, the more likely it was to have a greater number of locations, it provided a

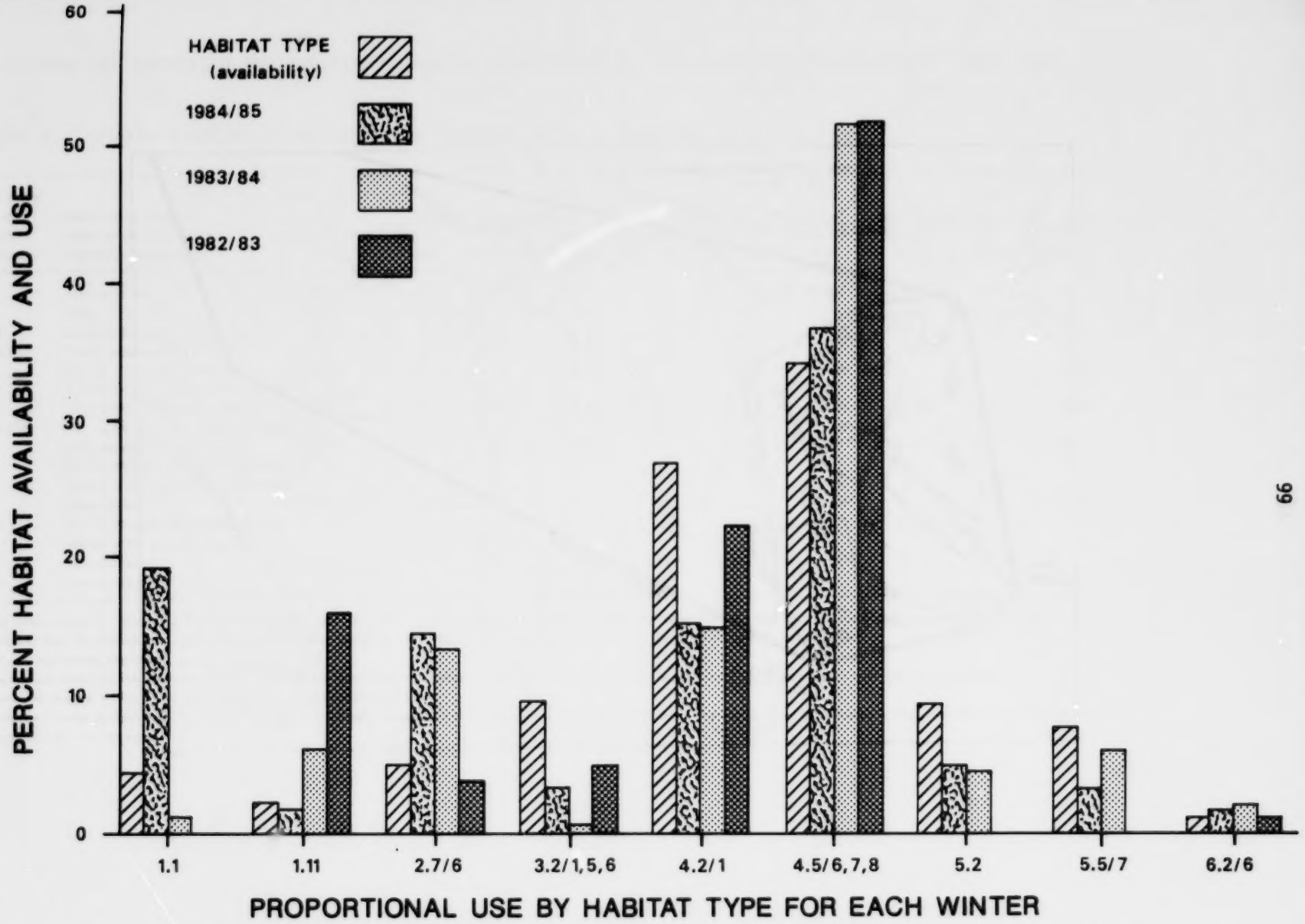

Figure 21. Availability and use for each habitat type for the Greenstone herd during mild and moderate winters. (See Table 2 for explanation of habitat type descriptions.)

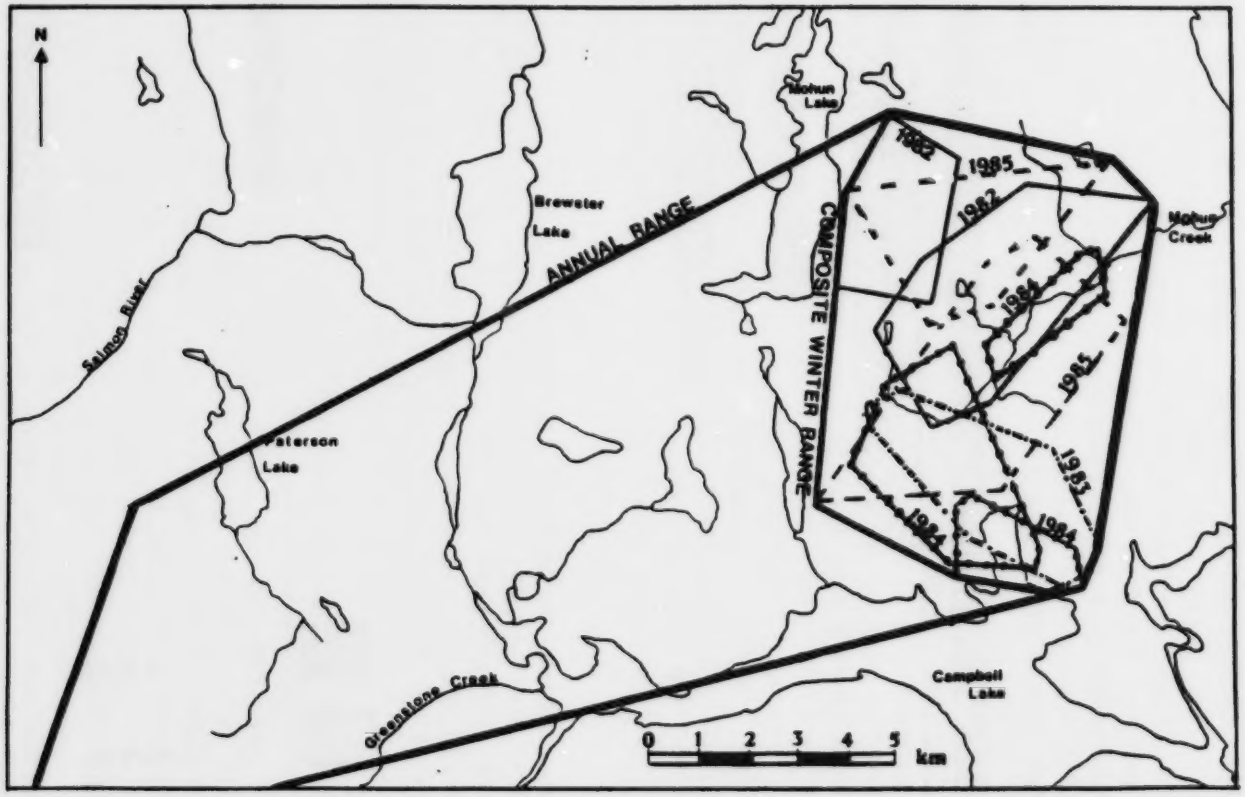

Figure 22. Composite and individual winter ranges used by elk of the Greenstone herd, 1981-1985.

Table 41. Winter habitat selection based on expected use compared to actual use

Major stand type and ecosystem association[1]	Descriptive name for major stand type and ecosystem association	Availability[2] (ha)	1984/85 (Moderate Winter)			1983/84 (Mild Winter)			1982/83 (Mild Winter)		
			Expected Use[3]	Actual Use[4] (n=125)	Selection Index[6]	Expected Use	Actual Use (n=180)	Selection Index	Expected Use	Actual Use (n=187)	Selection Index
1.1	Rock outcrops	200.5	5	24	4.8	8	2	0.25	8	0	0
1.11	Bogs	103.8	3	2	0.667	4	11	2.75	4	30	7.5
2.7/6	Deciduous-conifer complexes	227.0	6	18	3.0	9	24	2.67	9	7	0.777
3.2/1,5,6	Young regenerating conifer stands (1- to 20-year-old)	439.4	12	4	0.333	17	1	0.053	17	9	0.529
4.2/1	21- to 60-year-old conifer stands with drier ecosystem assoc.	1265.0	34	19	0.559	48	27	0.5625	48	42	0.875
4.5/6,7,8	21- to 60-year-old conifer stands with moister ecosystem assoc.	1604.5	43	46	1.07	61	93	1.52	61	97	1.59
5.2	21- to 40-year-old spaced conifer stands with a drier ecosystem association	442.7	12	6	0.5	17	8	0.470	17	0	0
5.5/7	21- to 40-year-old spaced conifer stands with moister ecosystem associations	359.8	10	4	0.4	14	10	0.714	14	0	0
6.2/6	Old growth	48.6	1	2	2.0	2	2	2.0	2	2	1.0

[1]Major stand types and ecosystem associations, combined. The first number indicates the stand type, the second number the most abundant ecosystem association. Numbers following the "/" indicate ecosystem associations that occur in that stand type in minor amounts (see Table 2 for further detail).

[2]Availability across the entire winter range (ha).

[3]Expected use based on the average number of locations (locations per hectare) that would occur if habitat use was distributed evenly over the winter range.

[4]Actual use (number of locations per hectare) from radio-collared elk.

[6]"Selection" index derived from dividing the number of actual locations by the number of expected locations. Any number over 1 indicates a positive selection, less than 1 avoidance, and 1 as no selection.

Table 42. Winter habitat selection based on Strauss' linear model

Stand type & ecosystem associations	Descriptive name for major stand type and ecosystem associations	Availability (proportional)	Use 1984/85 (Mod. Winter)	Significant difference[1]	Use 1983/84 (Mild Winter)	Significant difference	Use 1982/83 (Mild Winter)	Significant difference
1.1	Rock outcrops	.043	.192	+	.011	0	0	-
1.11	Bogs	0.0222	.016	0	.061	0	.160	+
2.7/6	Deciduous-conifer complexes	0.048	.144	+	.133	+	.037	0
3.2/1,5,6	Young regenerating conifer stands (1- to 20-year-old)	0.094	.032	0	.005	-	.048	0
4.2/1	21- to 60-year-old conifer stands with drier ecosystem assoc.	.270	.152	-	.15	-	.224	0
4.5/6,7,8	21- to 60-year-old conifer stands with moister ecosystem assoc.	.342	.368	0	.517	+	.519	+
5.2	21- to 40-year-old spaced conifer with a drier ecosystem association	.094	.048	0	.044	0	0	-
5.5/7	21- to 40-year-old spaced conifer with moister ecosystem associations	.077	.032	0	.06	0	0	-
6.2/6	Old growth	.01	.016	0	.02	0	.0111	0

[1]significance level of .10<p<.20. "+" denotes positive selection. "—" denotes negative selection, and "0" indicates no selection.

Table 43. Winter habitat selection assuming all habitats were equally used

Stand type & ecosystem association	Descriptive name for major stand type and ecosystem associations	Availability (proportional)	Expected[1] Use 1984/85	Actual Use 1984/85 (Mod. Winter)	Expected Use 1983/84	Actual Use 1983/84 (Mild Winter)	Expected Use 1982/83	Actual Use 1982/83 (Mild Winter)
1.1	Rock outcrops	.043	14	24[2]	20	2	21	0
1.11	Bogs	.022	14	2	20	11	21	30[2]
2.7/6	Deciduous-conifer complexes	.048	14	18[2]	20	24[2]	21	7
3.2/1,5,6	Young regenerating conifer stands (1- to 20-year-old)	.094	14	4	20	1	21	9
4.2/1	21- to 60-year-old conifer stands with drier ecosystem assoc.	.270	14	19[2]	20	27[2]	21	42[2]
4.5/6,7,8	21- to 60-year-old conifer stands with moister ecosystem assoc.	.342	14	46[2]	20	93[2]	21	97[2]
5.2	21- to 40-year-old spaced conifer with a drier ecosystem association	.094	14	6	20	8	21	0
5.5/7	21- to 40-year-old spaced conifer with moister ecosystem associations	.077	14	4	20	10	21	0
6.2/6	Old growth	.01	14	2	20	2	21	2

[1]expected use - equally dividing number of locations among habitat.
[2]indicates selection.

threshold value of a minimum number of locations a habitat must have to be selected (see Appendix 1).

Comparing these three indices gave a better estimate of selection or preference than if just one index was used (Table 44). Because of the bias involved in each index used, all three were presented for comparison in accurately reflecting habitat selection. The proportional use index (Table 41), suggested that rock outcrops, deciduous-conifer complexes, and 21- to 60-year-old conifer stands with moister ecosystem associations were preferred during the moderate winter (1984/85) while bogs and deciduous-conifer complexes were preferred during milder winter conditions (1982/83 and 1983/84). The linear index (Table 42) suggested that rock outcrops and deciduous-conifer complexes were significantly preferred; there was a statistical difference between the proportion that was available and the proportion that was used during moderate winter conditions. Selection in mild winter conditions indicated preferences for bogs, deciduous-conifer complexes, and 21- to 60-year-old conifer stands with moister ecosystem associations (both Moss - *Mahonia* and fern ecosystem associations). The third index (Table 43) indicated that bogs, deciduous-conifer complexes, and 21- to 60-year-old conifer stands with both moister and drier (*Gaultheria*) ecosystem associations were selected during the mild winter. Habitat selection shifted to rock outcrops from bogs in moderately severe winter conditions with continued use of deciduous-conifer complexes and 21-to 60-year-old conifer stands.

Several significant habitat selection trends were observed. Although it could be argued that selection of a home range which included each of these habitat types was, in fact, a selection of every habitat type in the home range, selection indices suggested otherwise. Habitat types of 21- to 40-year-old spaced conifer stands with 0.5 - 1.5 m debris depths and 1- to 20-year-old conifer stands were not selected using any of the indices. None of these habitat types received the expected amount of use even if all habitat use was equally divided (Table 43). Often, these habitats had larger areas available than some habitats that received greater than expected use. For example, bogs and rock outcrops had less area available than 1- to 20-year-old conifer stands and spaced stands, yet were used more often. The other selection indices indicated no preference whatsoever, or selection proportionally less than half of availability of 1- to 20-year-old conifer stands and spaced stands. Similar to the present study, Leckenby (1984) found that man-made forage areas (1- to 20-year-old conifer stands) were used less (17%) than they occurred, and natural forage areas were used more (83%). These findings suggest that retaining the integrity of natural forage areas (such as bogs) is important in maintaining and increasing elk use of critical winter ranges (see Section 4.7.4.3).

In all winters, old growth was selected for. However, low availability of old growth (1%), the small size of individual stands, and the dispersion of

Table 44. A comparison of all three selection indices for the moderate and mild winters

Major stand type and ecosystem associations	Descriptive name for major stand type and ecosystem associations	Availability (proportional)	Selection Indices 1984/85 (Moderate Winter)			Selection Indices 1983/84 (Mild Winter)			Selection Indices 1982/83 (Mild Winter		
			Proportional[1] expected use	Strauss[2] linear model	Equally[3] expected use	Proportional expected use	Strauss' linear model	Equally expected use	Proportional expected use	Strauss linear model	Equally expected use
1.1	Rock outcrops	.043	+[4]	+	+	-	0	0	-	-	-
1.11	Bogs	.022	-	0	0	+	0	0	+	+	+
2.7/6	Deciduous-conifer complexes	.048	+	+	+	+	+	+	-	0	0
3.2/1,5,6	Young regenarating conifer stands (1- to 20-year-old)	.094	-	0	0	-	-	0	-	0	0
4.2/1	21- to 60-year-old conifer stands with drier ecosystem assoc.	.270	-	-	+	-	-	+	-	0	+
4.5/6,7,8	21- to 60-year-old conifer stands with moister ecosystem assoc.	.342	+	0	+	+	+	+	+	+	+
5.2	21- to 40-year-old spaced conifer with a drier ecosystem association	.094	-	0	0	-	0	0	-	-	-
5.5/7	21- to 40-year-old spaced conifer with moister ecosystem associations	.077	-	0	0	-	0	0	-	-	-
6.2/6	Old growth	.01	+	0	0	+	0	0	+	0	0

[1]Selection based on expected proportional habitat use on the winter range (see Table 41).

[2]Selection based on Strauss' linear model (see Table 42).

[3]Selection based on equal habitat use on the winter range (see Table 43).

[4]"+" denotes positive selection; "-" denotes negative selection; "0" denotes no selection

those stands in the study area made it difficult to draw conclusions about the importance of old growth.

Mild winter habitat selection (1982/83 and 1983/84)

From Tables 41-44, the relative importance of bogs as preferred foraging areas in mild winters can be seen. Deciduous-conifer complexes also appear to be important in mild winters, as well as 21- to 60-year-old conifer stands with moister (Moss-*Mahonia*, *Blechnum*, or *Polystichum-Achlys*) ecosystem associations. These stands would probably increase in importance in more severe winters when less forage is available in more open stands because of snow burial. As previously mentioned, man-made openings (1- to 20-year-old conifer stands), and 21- to 40-year-old spaced conifer stands (made inaccessible by debris depths of 0.5 - 1.5 m), were avoided in mild winters and would probably be avoided in severe winters. As indicated in Section 4.7.4.3, home range sizes are inversely correlated to the proportion of bogs and deciduous-conifer complexes within a home range. These findings suggest that the carrying capacity of winter ranges in the study area used during mild winters would increase as the amount of foraging areas increases.

In mild winters, linear correlation analysis indicated a significant relationship ($p<.0025$, $r = .913$) between the number of locations per hectare by habitat type and the mean percent cover of sedges. Analyses of other habitat variables (canopy closure and mean percent cover of conifers, shrubs, forbs, grasses, and preferred forage species) show non-significant correlations with the number of locations per hectare ($p>.20$). The correlation of sedges can be explained by their occurrence in bogs and wetter habitats. Multiple regression models were used to examine the relationship between locations per hectare by habitat type and habitat variables (canopy closure and mean percent coverage of certain forage species). For mild winters, four habitat variables (canopy closure and percent cover of sedges, grasses, and western hemlock < 2m in height) explained 95% of the variation in habitat type use ($p<.05$) (Table 45). The combination of sedges, grasses, and canopy closure correlate with use because these forage species occur in bogs and wetter habitats where there is minimal canopy closure. Western hemlock seedlings (<2 m in height) grow well in shaded, moister ecosystem associations as found in 21- to 60-year-old conifer stands commonly found adjacent to bogs.

Moderate winter habitat selection (1984/85)

The shift in habitat use from bogs in mild winters to south aspect rock outcrops in the moderate winter is an obvious difference between the two types of winters. Although some forage (scattered grasses, some shrubs) is available on rock outcrops (and forage is buried by snow in bogs), the shift in habitat use is more likely related to solar conditions experienced on rock

Table 45. Habitat variables associated with locations per hectare during the winters of 1982/83, 1983/84, and 1984/85

Winter period	Habitat variables	r^2 (% variation explained)	Significance level	Partial correlation coefficient	Partial F value	Significance level
Mild winters 1982/83 and 1983/84 (all monitoring sessions)	Sedges	95	.025<p<.01	.0034	15.5	.01<p<.025
	Grasses			-.0148	7.0	.025<p<.05
	Canopy closure			-.0019	4.35	.05<p<.10
	Tsuga heterophylla				3.97	.05<p<.10
Moderate winter 1984/85 (all monitoring sessions)	Grasses	95	.001<p<.0025	.0072	70.99	
	Polystichum munitum			.0013	26.94	
Winter 1984/85 Monitoring session one (Nov 28-Dec 6, 1984)	Grasses	99	.005<p<.01	.002	443.15	.001<p<.0025
	Blechnum spicant			-.0146	72.0	.005<p<.01
	Polystichum munitum			.00098	65.81	.005<p<.01
	Sedges				51.7	.005<p<.01
Monitoring session two (Dec 30/84-Jan 2, 1985)	Sedges	99	.001<p<.0025	-.00015	88.81	.001<p<.0025
	Grasses			.0007	57.57	.001<p<.0025
	Mahonia nervosa			-.0011	48.06	.0025<p<.005
Monitoring session[1] three						
I (Feb 5 - 8/85)	Grasses	92	.005<p<.01	.0009	40.7	.001<p<.0025
	Sedges			.0006	6.2	.025<p<.05
II (Feb 9 - 10/85)	Grasses	99	p<.0005	.002	439.4	p<.0005
	Sedges			-.0001	40.76	.001<p<.0025
III (Feb 10 - 13/85)	*Polystichum munitum*	99	p<.0005	.0002	58.02	.001<p<.0025
	Blechnum spicant			-.0011	513.0	.025<p<.05
Total three (Feb 5 - 13/85)	Grasses	97	.0005<p<.001	.0028	120.41	p<.0005
	Sedges			-.0002	18.79	.005<p<.01
Monitoring session four (Feb 19/85)	*Polystichum munitum*	97	.01<p<.025	.0003	32.43	.005<p<.01
	Vaccinium spp.			-.002	14.95	.01<p<.025
	Sedges			-.0001	10.205	.01<p<.025

[1]Monitoring session three was divided into three parts because of the length of the session (with variable snow depths). It was then combined to give an overall analysis for the entire session of habitat variables associated with locations per hectare.

outcrops on sunny days. Solar radiation and its reflectance from snow covered surfaces when combined with the increased insulative properties of an animal's winter coat, is important in reducing heat loss during cooler winter temperatures (Parker and Robbins 1984). Solar radiation may increase the ability of an animal to withstand cold air temperatures and may potentially decrease metabolic rates (Grojean *et al.* 1980, cited by Parker and Robbins 1984). Rock outcrops may also offer favourable vantage points for earlier detection of predators and snow depths are reduced (due to melt) for easier mobility. Adjacent forested stands provide available forage and security cover.

Deciduous-conifer complexes were also important in moderate winters, along with 21- to 60-year-old conifer stands with Moss-*Mahonia* or fern (*Blechnum* or *Polystichum-Achlys*) ecosystem associations. These habitats would probably increase in importance during more severe winters when less forage is available in open sites. As previously mentioned, man-made openings (1- to 20-year-old stands) and 21- to 40-year-old conifer stands with backlog spacing debris were avoided and would probably be avoided in severe winters since any forage would be buried in the open sites, and debris and snow would limit forage availability in the stands. In mild winters, home range size was inversely correlated to the amount of bogs and deciduous-conifer complexes within the home range. Although sample size was limited for the moderate winter, this home range size relationship appears to be true for south-facing rock outcrops. For example, one elk's range consisted of 57% rock outcrops when snow accumulations were greater than 20 cm in depth (see Section 4.7.4.3).

In the moderate winter, the number of locations per hectare by habitat type for all monitoring sessions was significantly linearly correlated ($p<.025$, $r = .8006$) to mean percent coverage of grasses within a habitat type. In monitoring sessions one, two, and three, grasses were linearly correlated to locations per hectare for each session ($p<.025$, $p<.01$, $p<.0025$; $r = .84$, $.81$, $.91$, respectively). During monitoring session four, sword fern was linearly correlated ($p<.01$; $r = .86$) to locations per hectare by habitat type. The correlation of grasses can be explained by their occurrence on rock outcrops and the correlation of sword fern can be explained by its occurrence in moister conifer habitats which tended to be used more as snow depths increased.

For the moderate winter data, overall locations per hectare by habitat type (for all monitoring sessions), and individual locations per hectare by habitat type (for each monitoring session) were incorporated into multiple regression models as dependent variables. Independent variables were incorporated in two different ways. Locations per hectare by habitat type were initially regressed against forage availability after snowfalls. Results from these regression models were either not significant ($p>.10$) or, if significant ($.05<p<.10$), had very high standard errors, and often none of the partial regression coefficients were significant ($p>.25$). In general, a

significant multiple regression will be associated with at least some of the partial coefficients being significant (Zar 1974). Multiple regressions were then recalculated with forage availabilities before snow accumulation incorporated as independent habitat variables.

For the entire moderate winter, overall locations per hectare by habitat type were correlated to mean percent cover of grasses and sword fern ($.001<p<.005$) and explained 95% of the variation (Table 45). For monitoring session one, mean percent cover of deer fern, sword fern, grasses, and sedges was significant ($.001<p<.005$) and explained 99% of the variation in locations per hectare. In monitoring session two, mean percent cover of sedges, grasses, and Oregon-grape was significantly correlated ($.001<p<.0025$) and explained 99% of the variation in locations per hectare. Monitoring session three was first analysed as three separate periods (because of differing snow conditions and the different groups of elk) and then as one combined session. In periods I and II, mean percent coverage of grasses and sedges accounted for over 90% of the variation in locations per hectare ($p<.001$ and $p<.005$ significance levels, respectively), while period III had 99% of locations per hectare accounted for by sword fern and deer fern ($p<.0005$). Overall, monitoring session three (all periods combined) had 97% of variation in locations per hectare explained by mean percent coverage of grasses and sedges ($.0005<p<.001$). Monitoring session four had 96% of the variation in locations per hectare accounted for by mean percent coverage of sword fern, huckleberry, and sedges ($.01<p<.025$).

The overall correlation between locations per hectare by habitat type and the mean percent coverage of sword fern and grasses for the winter can be explained by the occurrence of grasses on rock outcrops and of sword fern in both 21- to 60-year-old conifer stands with moister ecosystem associations and deciduous-conifer complexes. All three types of habitats were preferred during the moderate winter. Habitat use of rock outcrops rather than bogs (as in mild winters) is reflected in the correlation of grasses (rather than sedges); increased use of forested habitat types is reflected in the correlation of sword fern.

Individual monitoring sessions were correlated with different forage species dependent on depth and duration of snow fall (see Section 4.2.2.1). Snow accumulations followed a pattern in which a brief accumulation period was succeeded by a meltdown period. This cycle of snowfall and snowmelt often limited the use of open habitats (such as bogs) for only short time periods.

In monitoring session one, grasses, sword fern, deer fern, and sedges correlated with locations per hectare. Ferns and sedges were used in 21- to 60-year-old conifer stands and deciduous-conifer complexes with moister ecosystems (especially areas with small seepage sites); grasses correlated with use on rock outcrops. Monitoring session two indicated the same trends of use shifting from open to canopied habitats and from bogs to rock

outcrops: in forested habitats, use correlated with Oregon-grape; in wetter areas of deciduous-conifer complexes, with sedges; and around rock outcrops, with grasses. In monitoring session three, grasses and sedges correlated with use during the initial stages of the monitoring session (periods I and II) when snow accumulations were less. Ferns correlated with use when snow depths were greater and there was increased use of forested habitats (period III). Monitoring session four followed the same trends with ferns and shrubs correlating with use in forested habitats, when snow accumulations were greater, and sedges correlating with use in wet areas in deciduous-conifer complexes.

Overall, locations per hectare appeared to correlate with forage that would be available given the snow conditions at the time of the monitoring session. Use of forage available in open and canopied habitats in each monitoring session reflected changing snow depths; the greater the snow depths, the more that habitats still having preferred forage species available were used. Use of rock outcrops, adjacent to 21- to 60-year-old conifer stands that still had forage available, also increased.

Distance to edge use

Distance to an open area (defined as bogs, rock outcrops, and 1- to 20-year-old conifer stands) was evaluated from radio-locations (n=132) in forested stand types (Figure 23). The mean distance from cover to forage areas was 143 m. Eighty percent of locations occurred within 200 m of a forage edge. Approximately 50% of the area of the Greenstone winter range used during 1982/83 and 1983/84 was greater than 200 m from a forage edge. Because locations in bogs constituted most locations in open habitats, and bogs were rarely larger than 100 m wide, it was difficult to derive a minimum distance to a forested edge from an open area. Recent clearcuts (1- to 20-year-old conifer stands) that were wider than bogs were rarely used. For comparison, distance to edge values from summer data (see Section 4.7.3) were added to give comparative values on distances to forested edges from open areas (Figure 23).

During the moderate winter of 1984/85; most of the locations (75%) that occurred on or near rock outcrops were within 100 m of the forested edge. Locations in 21- to 60-year-old conifer stands were within 100 m of the nearest rock outcrop and locations that occurred on rock outcrops were within 100 m of the forested edge. Most locations on rock outcrops were adjacent to 21- to 60-year-old conifer stands with a *Gaultheria* ecosystem association. Few locations occurred near other types of habitats adjacent to rock outcrops and only 25% of locations on rock outcrops occurred greater than 100 m from a forested edge. This indicates the importance not only of rock outcrops in moderate winters, but also of the adjacent stands and the interspersion of the two habitat types. Extremely large rock outcrops may not have been fully used because of the distance from a forested edge to the

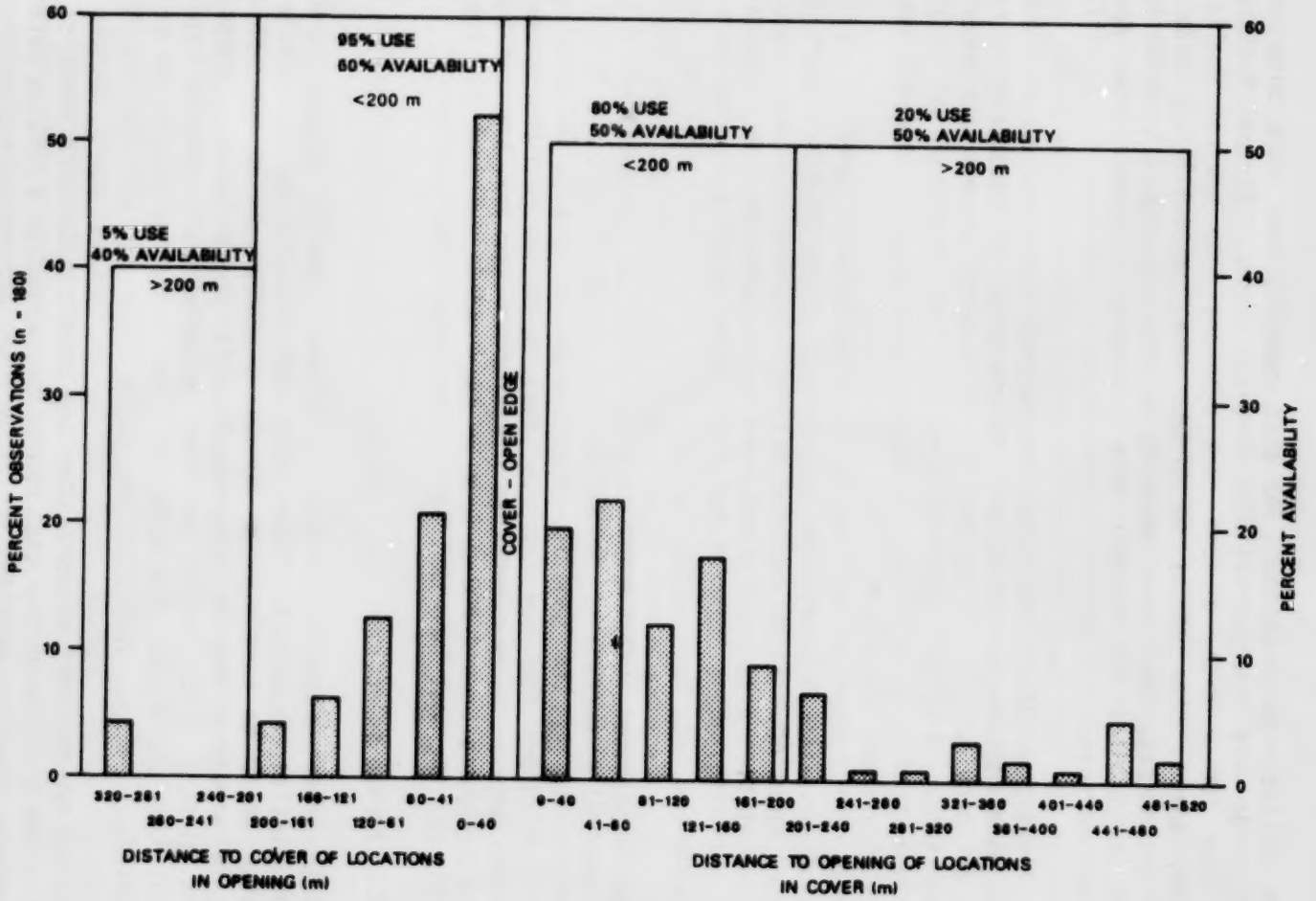

Figure 23. Frequency histogram of distance to openings and distance to cover from radiolocations collected from the Greenstone herd on the winter range and the Grilse herd on the summer range, respectively. Availability of forested stands and of open stands on each range are also included.

centre of the rock outcrop. The most commonly used rock outcrops on the winter range were interspersed with forested stands. Strips of timber, often less than 100 m wide, divided rock outcrops into several smaller areas. However, since these strips of timber were too small to classify as a separate habitat, they were included in rock outcrop classifications--even though the habitat was actually more a complex of timber cover patches and rock outcrops.

These findings indicate that both rock outcrop complexes and adjacent conifer stands with moister ecosystems are important to elk because both forage and cover are provided. Limiting the size of openings around rock outcrops would be important. Most rock outcrops used were less than 0.05 km^2 in size; many were less than 0.01 km^2 and, if larger, were usually long and narrow with widths no greater than 150 m.

Limiting the size of openings adjacent to bogs is also important. For example, creating a large clearcut beside a bog would increase total opening size. Most bogs used in mild and moderate winters were less than 0.04 km^2 in size; bogs (including adjacent openings) much larger than that were not used as frequently.

It should be noted that the accuracy of radiolocations obtained in this study were generally considered to be within 50-100 m of the true location. Therefore, it is the general relationships of Figure 23 that should be considered rather than the absolute level of use in 40-m increments that are indicated here. It is clear that use of both open and forested habitats is severely reduced beyond 200 m from an edge and it is this relationship that probably has the most important habitat management implications.

4.7.4.2 Forage selection

Strauss' linear selection index (1979) was used to assess selection for forage species. Strauss' index, although affected by unequal abundances, appears not to be as biased as Johnson's (1980) ranking approach which was used in previous project progress reports (Youds *et al.* 1985). (Bias caused dietary items, which occurred in very small amounts, to be often indicated as preferred. See Appendix 1 for a further discussion of selection indices).

Diets can be analysed at more than one level. The occurrence of a forage item in any quantity in the diet can be considered as a type of selection. In this study, however, availability of an item was considered in the analyses. For example, if an item occurred in 1% of the diet but covered 95% of the animals' range, it might not have been preferred. However, if the item is critical to the animal in only small amounts, even though usage is less

than availability it cannot necessarily be concluded that the item is not being selected for.

To determine which forage items were selected over others, the selection index was used to reduce the effects of unequal availability and show actual preference or avoidance. However, selection values could still reflect availability. For example, if sedges were preferred but buried by snow, the selection values would actually represent what was used from the forage left available. These analyses also defined the types of habitats that produce selected forage items and offer another method of determining preferred or critical habitat types.

Mild winter forage selection (1982/83 and 1983/84)

Availability of forage species for mild winters was determined from permanent plots in different habitat types on the winter range (Tables 46 and 47). Forage items are listed by percent occurrence in the diet for the mild winters and by selection values in Tables 48 and 49, respectively. Preferred diet species were determined by Strauss' linear index (Strauss 1979). Using this index, western hemlock was selected for during both mild winters. This species was used in proportions greater than its abundance on the winter range. In mild winters, no shrubs were selected for but sedges and grasses were selected for, coinciding with extensive use of bogs. Twinflower (*Linnaea borealis*) and deer fern, which occurred in 21- to 60-year-old conifer stands with moister ecosystems, were also selected for. This agrees with selection analyses which indicate that elk selected habitats providing these preferred forage species (see 'Mild winter habitat selection' Section 4.7.4.1).

Moderate winter forage availability (1984/85)

Permanent plots, established throughout the winter range, were visited after each snowfall event in the moderate winter (1984/85) to assess the relative abundance of forage in different habitat types (see Tables 46 and 47). Comparative baseline data on site characteristics and forage availability have been collected in previous years.

Vegetation availability was compared on an individual species basis and in combined forage class categories of conifers, shrubs, forbs, ferns, and grasses. Forage class comparisons (using chi-square and t-test statistics) of availability before and after snowfall events of greater than 20 cm in depth indicated significant differences in both open forested habitats ($p<.001$). When individual species were compared within forage classes in habitats with overstory canopies, significant differences between availability before and after snowfall events were found only in forb, fern, and grass species; individual shrub and conifer species were relatively unaffected by the amount of snow accumulation in canopied habitats. In open habitats, such as

Table 46. Mean percent coverage of forage classes (<2m) in stand types and ecosystem associations on the winter range

Major stand type and ecosystem associations	Descriptive name for major stand type and ecosystem associations	Availability (proportional)	Mean percent cover				
			Conifers	Shrubs	Forbs	Ferns	Grasses
1.1	Rock outcrops	.043	.27	4.22	5.1	.33	15.2
1.11	Bogs	.022	.07	80.42	2.28	1.07	87.07
2.7/6	Deciduous-conifer complexes	.048	.82	10.81	.35	55.42	2.78
3.2/1,5,6	1- to 20-year-old young regenerating conifer stands	.094	20.15	69.25	20.43	2.99	4.49
4.2/1	21- to 60-year-old conifer stands with drier ecosystem assoc.	.270	3.6	68.5	1.7	1.1	.5
4.5/6,7,8	21- to 60-year-old conifer stands with moister ecosystem assoc.	.342	2.76	28.26	3.15	13.37	.26
5.2, 5/7	21- to 40-year-old spaced conifer stands[1]	.171	3.31	32.5	6.07	5.89	.60
6.2/6	Old growth	.01	— no data				

[1]Understory vegetation was virtually unobtainable in any spaced stand due to debris depths.

Table 47. Mean percent coverage of selected forage species (<2m) in stand types and ecosystem associations on the winter range[1]

Species	Rock Outcrops (1.1)	Bogs (1.11)	Deciduous-conifer complexes (2.7/6)	Young regenerating conifer stands (1- to 20-year-old) (3.2/1,5,6)	21- to 60-year-old conifer stands with drier ecosystem assoc. (4.2/1)	21- to 60-year-old conifer stands with moister ecosystem assoc. (4.5/6,7,8)	21- to 40-year-old spaced[2] conifer stands (5.2, 5/7)
Conifers							
Tsuga heterophylla			.39	2.17	.4	.97	.61
Thuja plicata		.07		.88	1.7	.6	1.21
Pseudotsuga menziesii	.07		.14	19.94	1.43	1.18	1.46
Shrubs							
Alnus sp.			.64	.03			
Arctostaphylos uva-ursi	.07				.07		
Mahonia nervosa			.43	2.42	6.43	7.23	9.3
Gaultheria shallon	.47	.25	.89	72.92	54.47	16.23	19.85
Myrica gale		41.32	.89				
Oplopanax horridus			4.53				
Paxistima myrsinites				.08	.10	.06	
Ribes bracteosum				.07			
Rosa spp.	.51			.18.23			
Rubus spp.	.33	.93	2.68	.05	.23 .14		
Salix spp.		.39		.05	.87	.85 .79	
Spiraea douglasii		11.21			.03 .36		
Symphoricarpos albus				.06	.17	.29	
Vaccinium spp.	.27		1.43	3.4	6.0	4.06 2.07	
Forbs							
Linnaea borealis				20.96	.63	.68	.89
Ferns							
Blechnum spicant			3.5				
Polystichum munitum	.07		51.5	.11	1.1	.06	.14
Pteridium aquilinum		1.07		3.05		12.56	2.32
Equisetum spp.		.07	.07			.71	3.43
Graminoids							
Grasses	15.2	4.86	1.41	.44	.5	.2	.36
Carex spp.		82.14	1.07				

[1]No data was available for the forage availability in old growth.
[2]Understory vegetation was virtually unobtainable in any spaced stand due to debris depths.

Table 48. Percent winter diet composition for the Greenstone herd for the mild winters of 1982/83 and 1983/84

Forage Class	Species	Winter 1982/83 Jan-Feb	Winter 1983/84 Dec-Jan-Feb
Conifers[1]	*Tsuga heterophylla*	23.9	19.9
	Pseudotsuga menziesii		.9
	Thuja plicata	1.2	3.2
	Pinus sp.		.1
Shrubs	*Vaccinium* spp.	3.1	.4
	Gaultheria shallon	3.4	9.0
	Mahonia nervosa		2.9
	Myrica gale	.5	
	Rubus sp.	.9	
	Acer macrophyllum		
	Alnus spp.	.3	
	Menziesia ferrugina		
	Oplopanax horridus		
	Paxistima myrsinites		
	Ribes spp.	.4	
	Rosa spp.		
	Salix spp.		
	Sambucus racemosa		
	Spiraea douglasii		
	Symphoricarpos albus		
	Sorbus sitchensis		
	Arctostaphylos uva-ursi		.4
Forbs	*Linnaea borealis*[2]	14.1	19.2
	Lysichitum americanum	.9	
	Achlys triphylla	.2	
	Viola sp.	.1	
Ferns	*Blechnum spicant*	8.7	5.9
	Polystichum munitum	2.5	
	Pteridium aquilinum	3.3	
	Athyrium filix-femina	.4	
	Equisteum sp.	3.8	
Graminoids	Grasses	20.2	9.4
	Carex spp.	11.9	20.0

[1]The conifer class includes litter and all available conifer forage below 2 m.

[2]*Linnaea borealis* is an evergreen, herb-like shrub (Hitchcock and Cronquist 1973) which was placed in the forb class because of its occurrence in the herb layer (after Walmsley *et al.* 1980).

Table 49. Diet selection for the mild winters of 1982/83 and 1983/84 for the Greenstone herd

Forage Class	Species	Winter 1982/83[1]	Winter 1983/84
Conifers[1]	*Tsuga heterophylla*	+	+
	Pseudotsuga menziesii	0	-
	Thuja plicata		0
Shrubs	*Alnus* spp.	0	
	Arctostaphylos uva-ursi		0
	Mahonia nervosa		-
	Gaultheria shallon	-	-
	Myrica gale	0	
	Oplopanax horridus		
	Paxistima myrsinites		
	Ribes bracteosum		
	Rubus sp.		
	Rosa spp.	0	
	Salix spp.	-	
	Spiraea douglasii		
	Symphoricarpos albus		
	Vaccinium spp.	-	-
Forbs	*Linnaea borealis*	+	+
Ferns	*Blechnum spicant*	+	+
	Polystichum munitum	-	-
	Pteridium aquilinum	0	
	Equisteum sp.	+	
Graminoids	Grasses	+	+
	Carex spp.	+	+

[1]Selection is based on Strauss' (1979) linear index; "+" denotes positive selection; "-" negative selection, "0" indicates no selection at a significance level of $.05<p<.10$.

bogs and rock outcrops, availability of shrubs, forbs, and grasses significantly differed from pre-snowfall abundance ($0.1<p<.025$). In 1- to 20-year-old conifer stands, snow accumulations did not significantly affect the availability of conifers and shrubs. Although the abundance of forbs was somewhat decreased, this change was also non-significant ($.10<p$). In deciduous-conifer stands, the availability of ferns, conifers, and shrubs was significantly reduced ($.01<p<.025$) following snowfall events.

Differences in forage availabilities were reflected in elk habitat use patterns (see 'Moderate winter habitat selection', in Section 4.7.4.1). Bogs received decreased use after snowfalls greater than 20 cm because of reduced forage availability. Conifer stands, with available conifer, shrub, and fern forage, received increased use after snowfalls. Rock outcrops provided little forage but had increased use compared to that in mild winters, probably because of favourable solar conditions and the relatively rapid snowmelt on these sites, which increased forage availability.

Although measurements indicated differences in forage availabilities before and after snow accumulation periods, the differences may not have caused any appreciable change in foraging behaviour by the elk. Temporary plots, established to help identify factors of habitat use that could not be obtained through radio-locations alone, showed the strategies that elk used to obtain forage. In areas where ferns were only partially covered by snow, animals simply brushed aside the snow to reach them. In bogs, when snow depths were greater than 20 cm, there was evidence of cratering to reach forage items. The elk were using areas that contained preferred forage items (i.e. bogs) less frequently, but still attempted to use specific forage species.

In general, conifer stands with canopy closures of between 60 and 90% were used primarily for browsing. Extensive browsing was noted on shrub species (such as Oregon-grape and huckleberry), conifer species (western hemlock), and ferns (sword fern). Rock outcrops were used mainly for bedding, with grazing limited to exposed grasses. Most rock outcrops used had a south aspect; the only north-facing rock outcrop offered an extremely advantageous outlook over the surrounding area (for protection against possible predators). Conifer stands adjacent to rock outcrops were used for browsing. A south-facing, 1- to 20-year-old conifer stand was used for bedding; in one area, 16 distinct bedding sites were noted and although forage species such as salal and huckleberry were available, there was little evidence of browsing. Bogs, although rarely used during periods of snow accumulation in the moderate winter, were used mainly for bedding and feeding activities. Extensive feeding occurred on both sedges and sweet gale (*Myrica gale*) in these areas. Often, snow had been brushed off to expose the green shoots beneath the dry tops of the sedges. Deciduous-conifer complexes were generally used for feeding, with deer fern and sword fern the major species browsed.

Moderate winter forage selection (1984/85)

Diet selection data were analysed separately for each monitoring session during the winter of 1984/85. Because of the differing snow conditions experienced during each monitoring session (see Section 4.2.2.1), diets were not combined for the entire winter. Rather, they were compared between monitoring sessions, using chi-square statistics by forage class categories (instead of by individual species because the low sample size in individual species violated the assumption of contingency tables that no expected frequency be less than 1.0, and that no more than 20% of the expected frequencies be less than 5.0 [Cochran 1977]). Although diets differed between monitoring sessions throughout the winter ($p<.05$), diets between different groups varied little within a monitoring session. These minor variations can probably be attributed to individual elk preferences.

Forage items that occurred in the diet are listed in Table 50 as a percentage of the total diet for that monitoring session. The diversity of forage items in the diet increases from mild winters to moderate winters; however, only 24 of the total number of species listed have been found in the permanent plots on the winter range. Since "non-occurring" species compose very little of the diet (usually less than 8%), use/availability analyses were completed on species for which abundance could be determined.

Food selection analyses for the moderate winter were calculated on the abundance of species in the diet before snowfall. Availability of most forage items in the conifer and shrub classes in conifer stands with canopy cover did not differ between snow-free and snow accumulation periods. However, forb, fern, and grass availability in the same settings did change between snow-free and snow accumulation periods, but the changes were not enough to keep these forage species from being used. When dietary use shifted from selected forage items between monitoring sessions, the shifts were assumed to be due to snow burial of certain forage items. Based on non-parametric and parametric statistics (Spearman rank and linear correlation analyses) and forage abundances before and after snowfall events, use/availability analyses indicated that dietary selection did not correlate to availability: the most available food items were not necessarily the most abundant in the diet.

On a percentage basis, shrubs and conifers dominated diets during snow accumulation periods, while grasses and ferns occurred in greater portions during snow-melt or snow-free periods (Table 48). Shrubs such as Oregon-grape, huckleberry, and salal were consumed in significantly greater proportions during snow accumulation periods than in snow-free or mild winter periods. Western hemlock was a significant proportion of the diet in both snow accumulation and snow-free periods. Twinflower, deer fern, and sedges declined in importance in snow accumulation periods, but were important dietary items in snow-free conditions.

Table 50. Percent winter diet composition for the Greenstone herd for the moderate winter of 1984/85

Forage Class	Species	One Nov.28-Dec.6 1984 30.5 cm[1]	Two Dec.30-Jan.2 1984/85 32.5 cm	Two Dec.30-Jan.2 1984/85 32.5 cm	Two Dec.30-Jan.2 1984/85 32.5 cm	Jan. 18, 1985[4] 20 cm	Three Feb.5-10/85 45.2 cm	Three Feb.9-13/85 45.2 cm	Four Feb.19/85 40.5 cm	Five[4] Feb.28/85 40.5 cm
Conifers[2]	*Tsuga heterophylla*	12.7	31.0	20.0	12.1	16.7	34.7	21.0	45.4	30.0
	Pseudotsuga menziesii	3.2	6.4	2.3	2.0	2.6		.8	1.2	3.2
	Thuja plicata	4.2	13.1	1.4	8.9	.8	2.3	3.5	2.4	1.2
	Pinus sp.									
Shrubs	*Vaccinium* spp.	19.1	24.5	16.7	9.2	9.6	17.6	17.1	11.8	5.1
	Gaultheria shallon	2.3	12.2	21.4	33.1	3.1	15.7	16.6	23.8	7.6
	Mahonia nervosa		4.6	4.8	4.8	2.4	.5	2.4	4.3	7.7
	Myrica gale									
	Rubus spp.				1.6	.7	.3	4.6	.7	.5
	Acer macrophyllum				.2		.6			
	Alnus sp.				.2					
	Menziesia ferruginea		.3		.4					1.1
	Oplopanax horridus									.3
	Paxistima myrsinites		.4	2.3		1.0		2.3	.2	.1
	Ribes spp.		.8				1.6		.4	.2
	Rosa spp.	.2	.2	.3	3.3					
	Salix spp.	1.4	1.5	.6	.2	.6		1.5	1.7	
	Sambucus racemosa	.1	.8	.3	.3		.5	3.0	.2	4.7
	Spiraea douglasii					.3		.3	.8	.5
	Symphoricarpos albus									.3
	Sorbus sitchensis		.3	.2						.5
	Arctostaphylos uva-ursi									
Forbs	*Linnaea borealis*[3]					7.6				17.5
	Lysichitum americanum									
	Achlys triphylla									
	Viola sp.									
Ferns	*Blechnum spicant*		1.8	13.0	11.4	20.7	3.6	3.8	.6	1.5
	Polystichum munitum		.6	6.9	.3	17.2		2.0		
	Pteridium aquilinum									
	Athrium filix-femina				.5	.8	.4	6.4		2.5
	Equisetum sp.	.7			.7					
		1.0								
Graminoids	Grasses	48.3		8.0	3.8	12.0	1.4	1.8	.4	4.5
	Carex spp.	.6		.2	5.4	1.9	20.3	6.8	5.5	10.2

[1]Mean snow depths at Morton Road Station.

[2]The conifer class includes litter and all available conifer forage below 2 m.

[3]*Linnaea borealis* is an evergreen, herb-like shrub (Hitchcock and Cronquist 1973) which was placed in the forb class because of its occurrence in the herb layer (after Walmsley *et al.* 1980).

[4]More than one group of animals in the Greenstone herd were monitored during some sessions therefore more than one diet is included for that time period.

[5]Snowmelt periods.

Changes in dietary items between moderate and mild winters corresponded to shifts in habitat use as discussed previously. Although species such as rose (*Rosa* spp.) and falsebox (*Paxistima myrsinites*) occurred in trace amounts during the moderate winter (1984/85), these types of dry site species which commonly occur on or near rock outcrops were not found in the diets during the mild winters (1982/83 and 1983/84). Their occurrence in the diet reflects a change in elk habitat use from wet bogs to drier rock outcrops during the moderate winter. Figure 24 depicts the relationships between snow depth and percent diet of graminoids (grasses and sedges) and conifers. Although elk are adapted to a grazing type of diet, browse (shrub and conifers) is used more extensively when graminoids are unavailable. Species commonly used in moister open site habitats (such as sedges in bogs) received little use during periods of snow accumulations, while species present in forested stands especially those adjacent to rock outcrops (such as Oregon-grape and huckleberry) received increased use. This indicates the importance of managing conifer stands near or adjacent to rock outcrops to ensure the forage production required in moderate or severe winters. Although rock outcrops provide some forage (mainly grasses), elk also use these habitats for favourable solar conditions and reduced snow depths.

Selection for particular forage species was determined by Strauss' linear index (Table 51). According to this, western hemlock was the most consistently selected species in both moderate and mild winters, always used in proportions greater than its abundance on the winter range. Douglas-fir was used only in proportion to its availability and western redcedar was only selected for during two monitoring sessions in the moderate winter. This may be due to low use of wetter habitats where cedar occurred. Huckleberry was the most preferred shrub in the moderate winter. Although salal and Oregon-grape were extensively used, the index did not indicate that they were selected for. Deer fern was the most preferred species of the fern class and was used even during snow accumulation periods. Sedges decreased in importance with increasing snow accumulations. Grasses were selected often in the moderate winter because of their occurrence on rock outcrops and availability during the rapid snowmelts which occurred on south aspect rock outcrops.

4.7.4.3 Relationships between forage and habitat components, and home range size

Area and proportion of habitat types within home ranges (encompassing 4- to 6-day monitoring sessions) were assessed during the winters of 1982/83, 1983/84, and 1984/85. Figure 25 depicts a frequency distribution of home range sizes (from monitoring sessions) for both mild and moderate winters, with an average size of 143.43 ha.

Cumulative home range sizes (all intensive monitoring sessions for each group combined) increased from the mild winters to the moderate winter. Cumulative

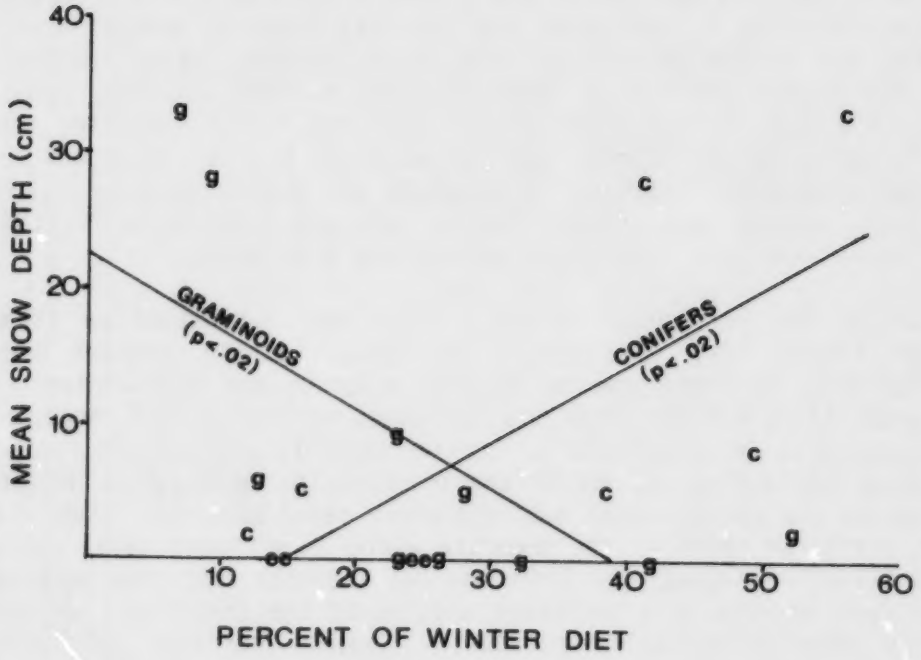

Figure 24. Relationships between percent graminoids in diet and snow depth (g), and between percent conifers in diet and snow depth (c).

Table 51. Diet selection[1] by intensive monitoring session for the winter of 1984/85 for the Greenstone herd

Species	MONITORING SESSIONS								
	One (Nov. 28 to Dec. 6/84)	Two[2] (Dec. 30 to Jan. 2, 84/85)	Two (Dec. 30 to Jan. 2, 84/85)	Two (Dec. 30 to Jan. 2, 84/85)	Jan. 18/85[3]	Three Feb. 5-10, 1985	Three Feb. 9-13 1985	Four[3] Feb. 19, 1985	Five[3] Feb. 28, 1985
Conifers									
Tsuga heterophylla	+ (+)	+ (+)	+ (+)	+ (+)	+ (+)	+ (+)	+ (+)	+ (+)	+ (+)
Thuja plicata	+ (0)	+ (+)	0 (-)	+ (+)	0 (-)	0 (0)	0 (0)	0 (-)	0 (-)
Pseudotsuga menziesii	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)		- (-)	0 (0)	0 (0)
Shrubs									
Alnus sp.				0 (-)			+ (0)		
Arctostaphylos uva-ursi				0 (-)			-		
Mahonia nervosa	- (0)	- (-)	- (0)	-	- (0)	- (0)	- (+)		
Gaultheria shallon	- (+)	- (+)	- (+)	- (+)	- (0)	- (+)		- (0)	0 (+)
Myrica gale				0 (-)				- (+)	0 (+)
Oplopanax horridus					0 (-)		+ (0)		
Paxistima myrsinites		0 (-)	+ (0)			+ (0)			0 (-)
Ribes bracteosum		0			0 (-)			0 (-)	0 (-)
Rosa spp.	0 (-)	0 (-)	- (-)	0 (-)		- (0)	0 (0)	0 (-)	0 (-)
Rubus spp.				0 (-)	0 (-)		+ (-)		
Salix spp.	+ (-)	+ (-)	0 (-)		0 (-)		0 (-)	0 (-)	0 (-)
Spiraea douglasii				0 (+)	0 (+)	+ (+)	+ (+)	+	0 (-)
Symphoricarpos albus		+ (+)	+ (+)					0 (-)	0 (-)
Vaccinium spp.									0 (-)
Forbs								+ (+)	0 (-)
Linnaea borealis									
Ferns								+ (+)	+ (+)
Blechnum spicant		0 (0)	+ (+)	+ (+)	+ (+)	+ (0)	+ (0)		
Polystichum munitum		- (-)	- (0)	- (-)	+ (+)		- (0)		
Pteridium aquilinum			0 (0)	0 (-)				0 (-)	0 (-)
Equisetum sp.	0 (-)								
Graminoids									
Grasses	+ (+)	- (-)	+ (+)	0 (0)	+ (+)	0 (-)	0 (-)	0 (0)	+ (+)
Carex spp.	- (-)	- (-)	- (-)	0 (0)	0 (0)	+ (+)	+ (0)	0 (0)	+ (+)

[1]Selection is based on Strauss' (1979) linear index; "+" denotes positive selection, "-" negative selection, "0" indicates no selection at a significance level of .05<p<.10. Values without brackets indicate selection when proportional abundances for each species are used. Values with brackets are when all species abundance are considered equal.
[2]More than one group of animals in the Greenstone herd were monitored during some sections therefore, more than one diet is included for that time period.
[3]Snowmelt periods.

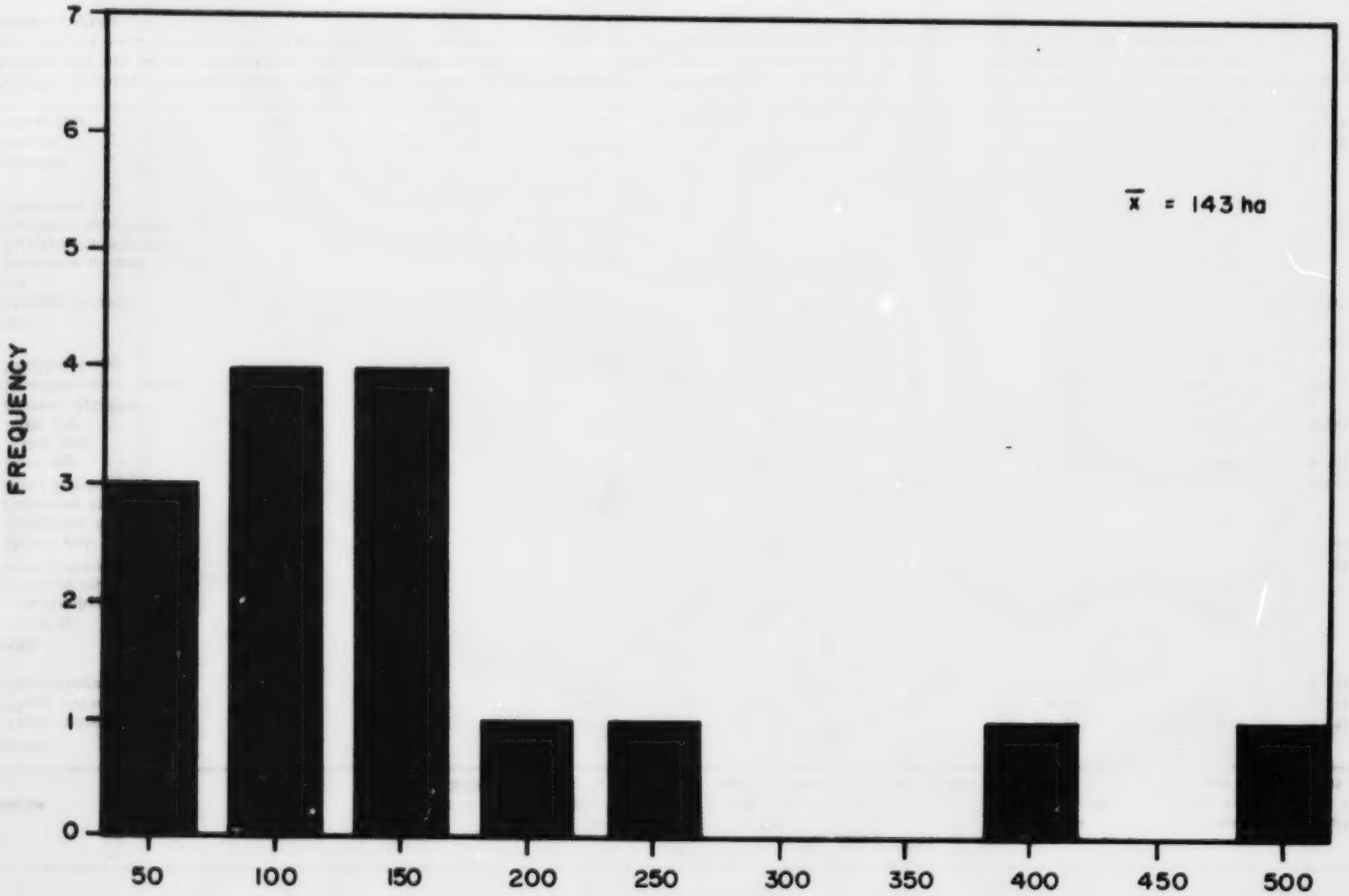

Figure 25. Frequency distribution of home range sizes from 4- to 6-day monitoring sessions of Greenstone herd elk during the winters of 1982/83, 1983/84, and 1984/85

home ranges sizes for the 1982/83 and 1983/84 winters were 787 ha and 898 ha, respectively. For the moderate winter of 1984/85, cumulative home range sizes averaged 1400 ha.

Mild winter home range size relationships

Intensive monitoring sessions with low or no snow accumulations were analysed separately from monitoring sessions with significant snow accumulations (i.e. greater than 20 cm). Although there were no differences in home range sizes between low or no snowfall periods as compared to snow accumulation periods, the specific habitat types used and their proportions did differ.

During low or no snow accumulation periods, linear regression analyses indicated home range sizes were significantly negatively correlated with the proportion of bogs ($.01<p<.025$) and the proportion of deciduous-conifer complexes ($.01<p<.025$) within the home range (Figures 26 and 27). These findings suggest that the suitability and carrying capacity of a mild winter range increase as the proportion of bogs and deciduous-conifer complexes within the range increases. Home range sizes were also related to the proportions of forage classes within the home ranges. Significant negative relationships ($.01<p<.025$) were shown between the proportion of graminoids within the home range and home range sizes. Non-parametric (Spearman rank correlation) tests indicated relationships between home range size and both shrub and grass forage classes ($p<.05$).

Linear and multiple regression analyses were used to relate proportion of forage species (rather than forage classes) to home range size. Proportions of forage class species were determined from cover values visually estimated in permanent plots in different habitat types on the winter range (see Section 3.2.1). Home range sizes were significantly negatively related to the proportion of sedges ($.01<p<.025$) in the home range (Figure 28).

In multiple regression analyses, the proportion of sedges and twinflower were significantly related ($.01<p<.025$) to home range size is as follows:

$$Y = 346.7 + (-22.1X_1) + (-22.8X_2);\ r = -.798;$$

where Y is the home range size, X_1 is the proportion of sedges in the home range, and X_2 is the proportion of twinflower in the home range. Since the coefficients for sedges and twinflower were almost equal, proportions were combined and a linear regression was run on the combined total. Home range sizes were significantly negatively related ($.0025<p<.005$) to the combined proportions of sedges and twinflower (Figure 29).

During mild winters, sedges and twinflower are preferred plant taxa and make up a major part of the diet (see Table 15). This relationship suggests that carrying capacity and suitability of a mild winter range increases as the

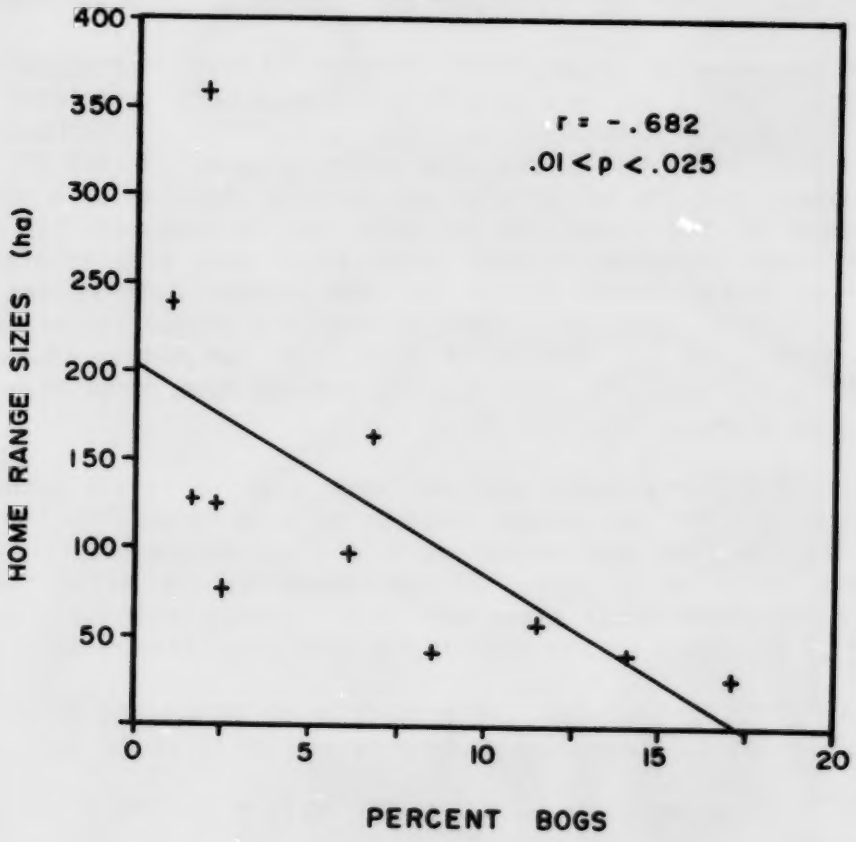

Figure 26. Relationship between 4- to 6-day home range sizes and the percent bogs within the home range.

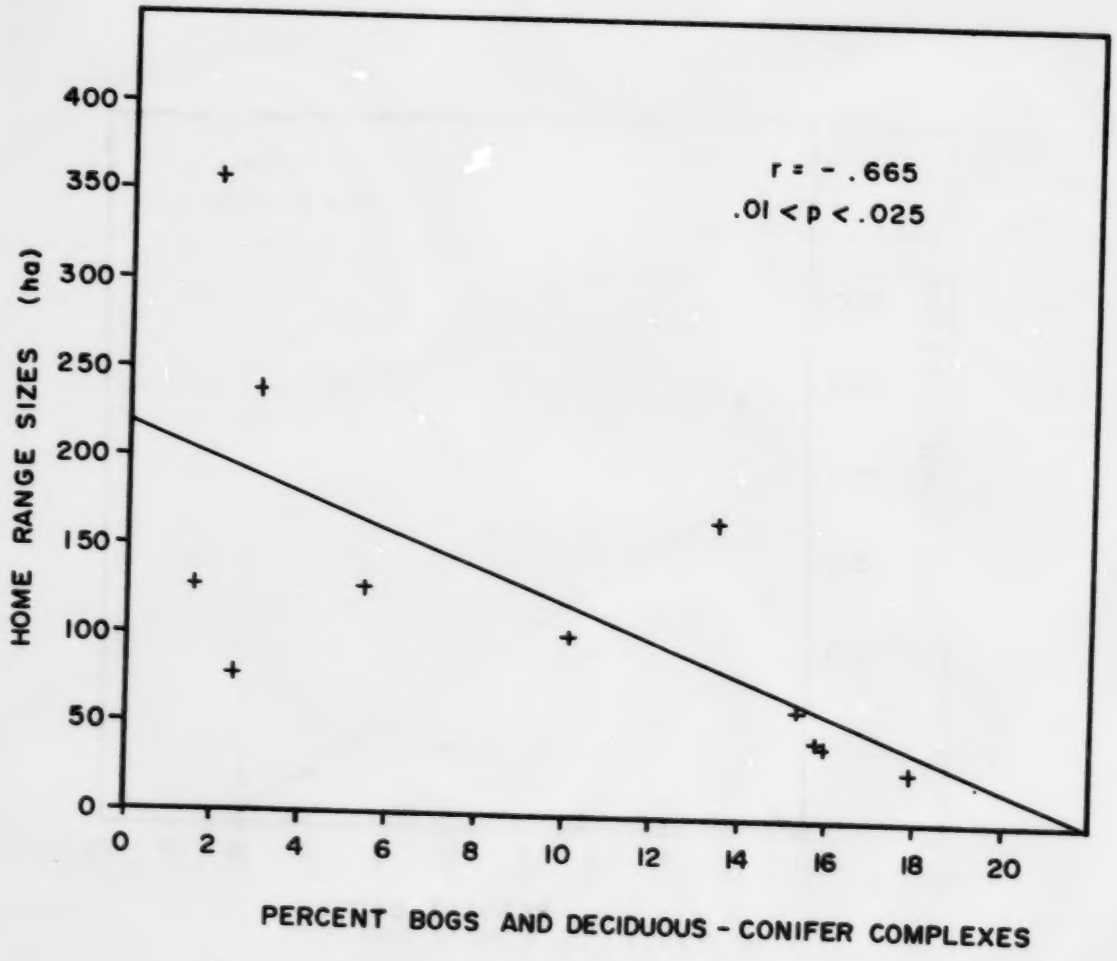

Figure 27. Relationship between 4- to 6-day home range sizes and the percent of bogs and deciduous-conifer complexes within the home range.

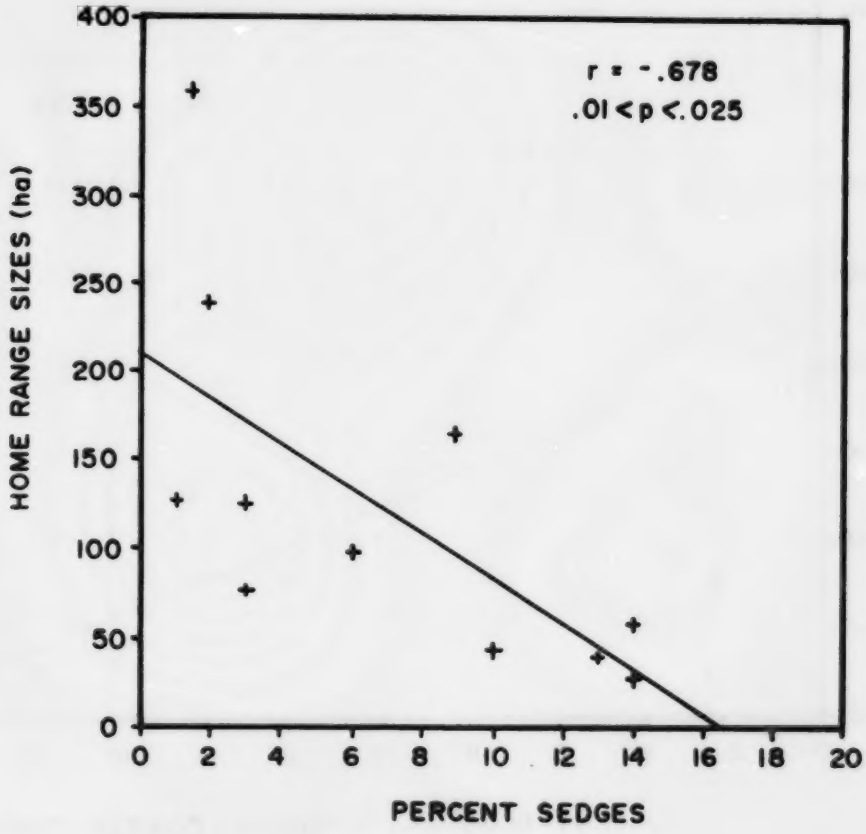

Figure 28. Relationship between 4- to 6-day home range sizes and the percent cover of sedges within the home range.

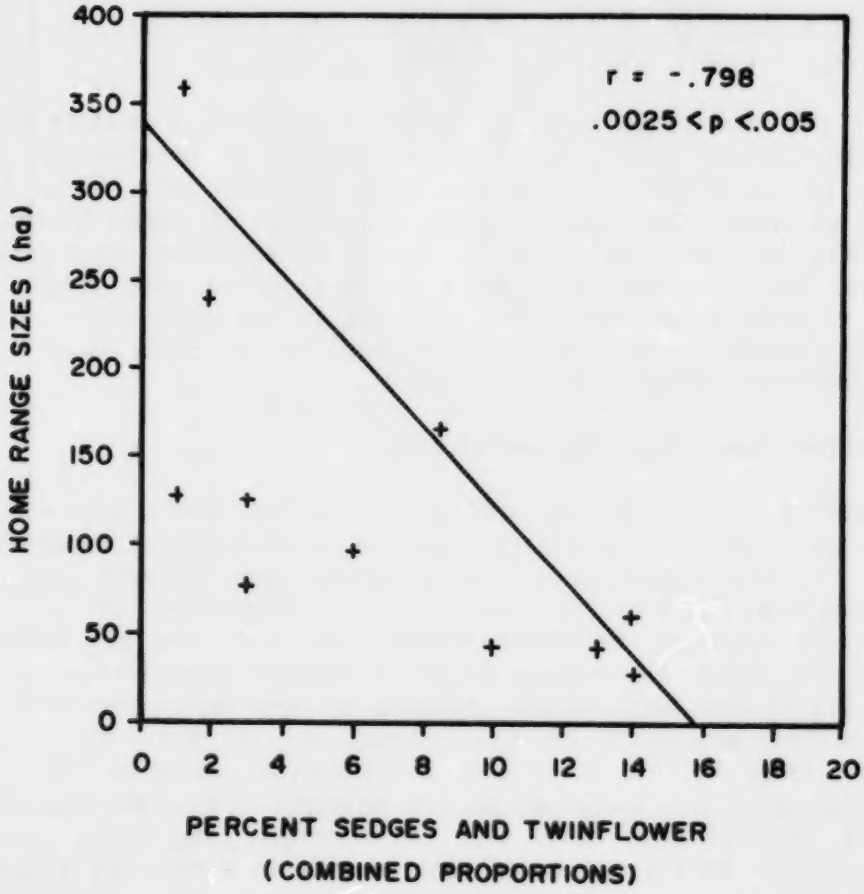

Figure 29. Relationship between 4- to 6-day home range sizes and the percent combined coverage of sedges and twinflower within the home range.

amount of available preferred forage increases, further identifying the importance of bogs as forage areas (since sedges grow mainly in bogs). Twinflower commonly occurs in 21- to 60-year-old conifer stands with Moss-*Mahonia* and *Vaccinium*-Moss ecosystem associations. These stands are often located adjacent to bogs.

Multiple regressions were further run, incorporating proportions of other dietary items. Significant relationships ($.01<p<.025$) were indicated between home range size during mild winter conditions and the proportions of western hemlock, salal, huckleberry, twinflower, deer fern, sword fern, and sedges, as follows:

$$Y = -130.02 + 1892.14X_1 + (-27.55X_2) + 119.52X_3 + (-43.03X_4) + (-774.0X_5) + (-67.77X_6) + (-40.6232X_7); \quad t = -0.985;$$

where Y is the home range size, X_1 is the proportion of western hemlock, X_2 is the proportion of salal, X_3 is the proportion of huckleberry, X_4 is the proportion of twinflower, X_5 is the proportion of deer fern, X_6 is the proportion of sword fern, and X_7 is the proportion of sedges within the home range. All partial coefficients for this equation were significant ($.01<p<.025$) and the equation appears to have fairly good predictive power when used on home range samples not included in the regression. Again, this relationship suggests that the carrying capacity increases as the amount of available preferred forage species increases.

Moderate winter home range size relationships

Although sample sizes were much smaller for periods where snow accumulations occurred, there was a significant negative relationship between home range sizes and (1) the proportion of south aspect rock outcrops and deciduous-conifer complexes ($.10<p<.25$), and (2) the proportion of all preferred habitats (rock outcrops, deciduous-conifer complexes, and 21- to 60-year-old conifer stands with *Polystichum-Achlys* ecosystem association) ($0.5<p<.10$) occurring within the home ranges (Figures 30 and 31). Figure 30 suggests that the maximum proportion of rock outcrops and deciduous-conifer complexes that a home range in this study area could contain would be 50%. Figure 31 suggests that with the inclusion of the moister, 21- to 60-year-old conifer stands, the smallest home range size could contain only these three habitat types and fulfill forage and cover requirements in a moderate winter. Thus, maximizing the amounts of these habitat components could possibly increase the carrying capacity of a winter range.

Relationships between proportions of available forage and home range sizes for moderate winter conditions could not be fully analysed because of the small sample size.

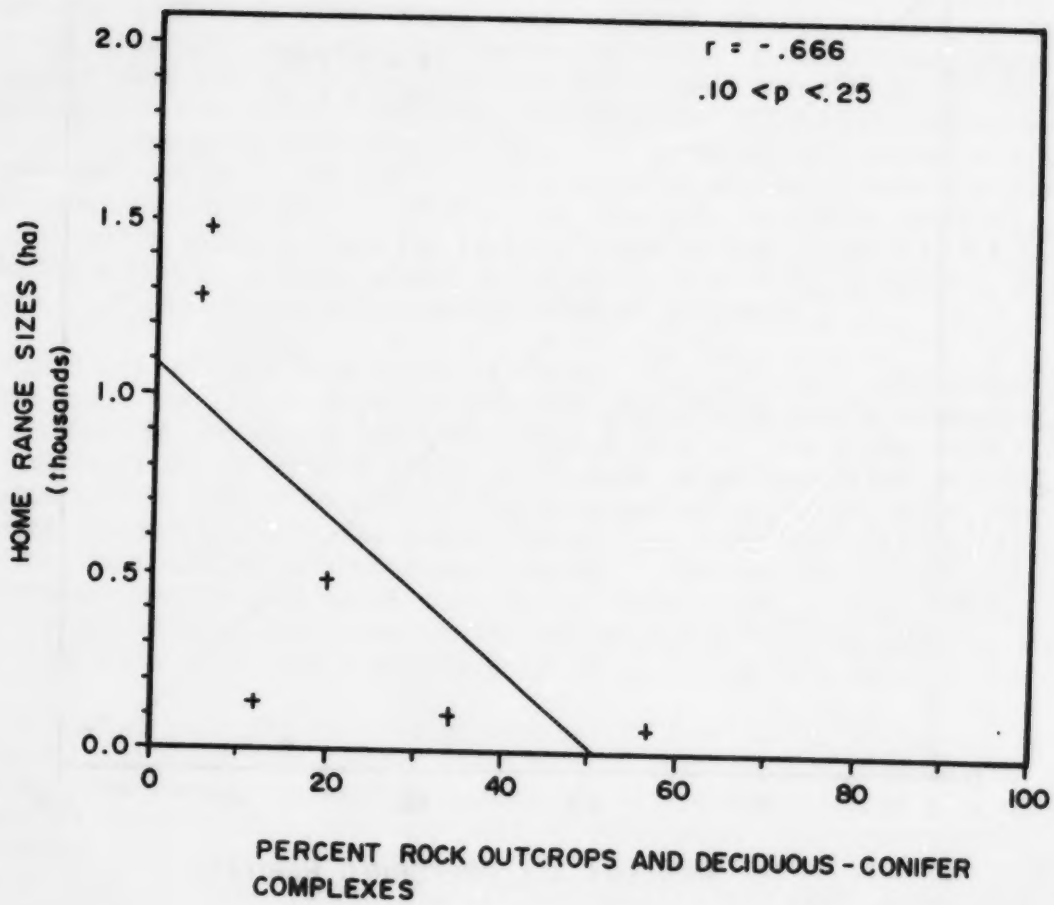

Figure 30. Relationship between 4- to 6-day home range sizes and the percent of rock outcrops and deciduous-conifer complexes within the home range.

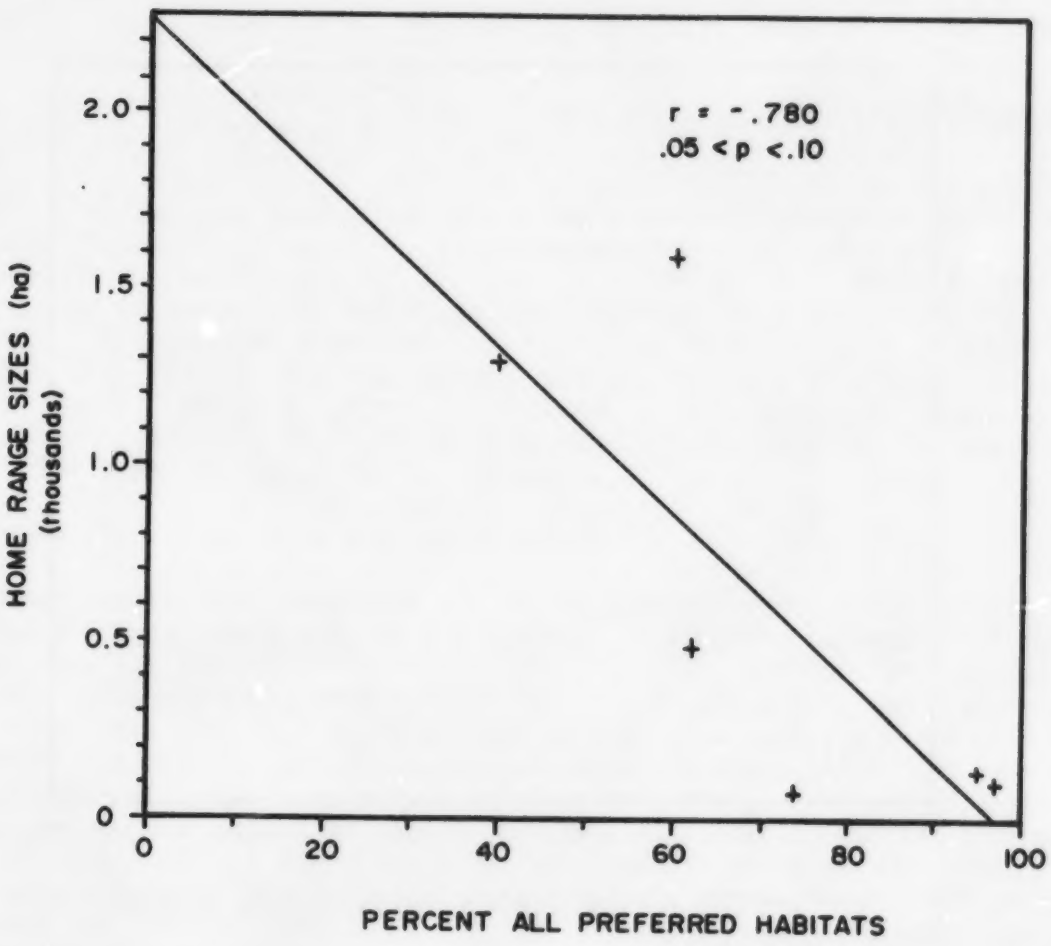

Figure 31. Relationship between 4- to 6-day home range sizes and the percent preferred habitats within the home range. Preferred habitats include rock outcrops, deciduous-conifer complexes and 20- to 60-year-old conifer stands with *Polystichum-Achlys*, *Blechnum*, and Moss-*Mahonia* ecosystem associations.

Winter home range size relationships with specific habitat components

Relationships were assessed between 4- to 6-day home range sizes and the proportion of conifer stands and the proportion of non-conifer stands (bogs, rock outcrops, and deciduous-conifer complexes) encompassed by the home range. Percent conifer stands versus percent non-conifer stands with home range sizes are depicted in Figure 32. The actual proportion of each habitat type on the overall winter range (11% combined bogs, rock outcrops, and deciduous-conifer complexes and 89% conifer stands) is indicated. Sizes of home ranges that encompassed a smaller proportion of conifer stands were compared with home range sizes that included greater amounts of conifer stands than were available on the entire winter range. Home ranges with greater than 11% non-conifer habitats had a mean size of 80 ha, while the average for home ranges that contained more than 89% conifer stands was 216 ha. The two means were compared using the non-parametric analog to a t-test (Mann-Whitney test) (Zar 1974), which indicated the means were significantly different ($.010<p<.025$). Similar to previous regression analyses, this relationship suggests that the carrying capacity and suitability of an area during a mild to moderate winter increases relative to the proportion of bogs, rock outcrops, and deciduous-conifer complexes available.

Proportions of preferred habitats (bogs, rock outcrops, deciduous-conifer complexes, and 21- to 60-year-old conifer stands with moister ecosystems) are depicted in frequency distributions within 4- to 6-day home ranges (Figures 33-35). Over half (nine) of the home ranges encompassed at least some proportion ($\geq$ 13%) of bogs and/or rock outcrops as their total area. This is a higher proportion than the proportion of bogs and rock outcrops available across the entire winter range (6.5%). Non-conifer stands (including deciduous-conifer complexes) made up at least 14.9% of home ranges. All preferred habitats (including conifer and non-conifer stands) comprised 20-100% of home range areas with a mean coverage of 56% of the home range.

Figure 36 depicts the relative proportions of open (1- to 20-year-old conifer stands) and cover (any conifer stand over 20 years of age) areas within 4- to 6-day home ranges, as well as across the entire winter range (20% openings and 80% cover areas). The mean size of home ranges with proportionally more openings than available on the winter range was smaller (125 ha) than the mean size of home ranges with proportionally less open areas (156 ha). However, there was no significant difference between the means ($p>.20$).

Figure 37 depicts the relative proportion of preferred habitats (non-conifer habitats and 21- to 60-year-old conifer stands with moister ecosystem associations) and avoided habitats (1- to 20-year-old conifer and 21- to 40-year-old conifer stands with backlog spacing debris) within 4- to 6-day home ranges and across the entire winter range (44% preferred habitats and 56% avoided habitats). The mean size of home ranges containing greater proportions of avoided habitats than occurred across the winter range was

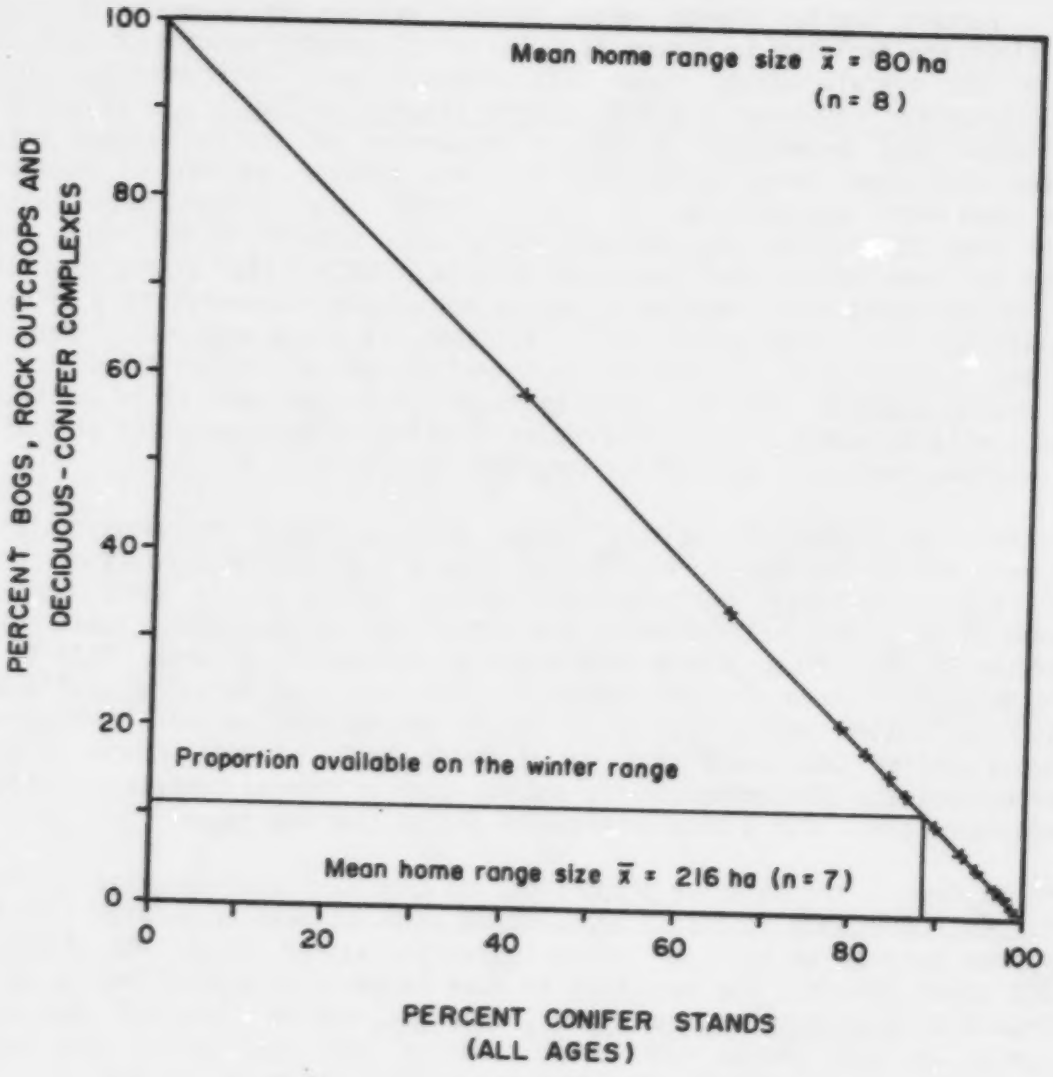

Figure 32. The relative proportion of conifer and non-conifer stands (bogs, rock outcrops, and deciduous-conifer complexes) within 4- to 6-day home ranges. Mean sizes of home ranges with greater and lesser proportions than occurred across the winter range are also indicated.

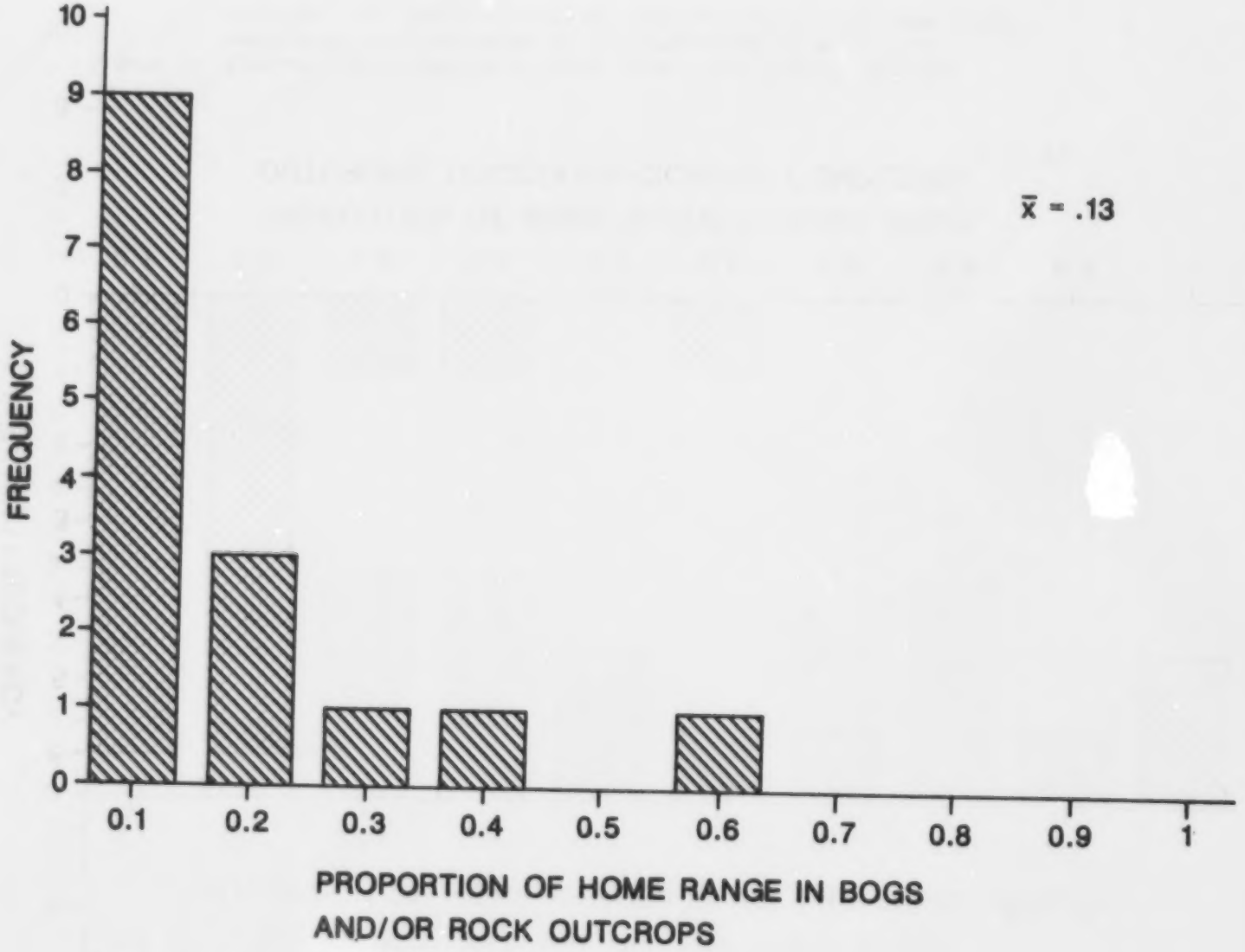

Figure 33. Frequency distribution of home range sizes from 4- to 6-day monitoring sessions based on the proportion of bogs and/or rock outcrops contained in the home range.

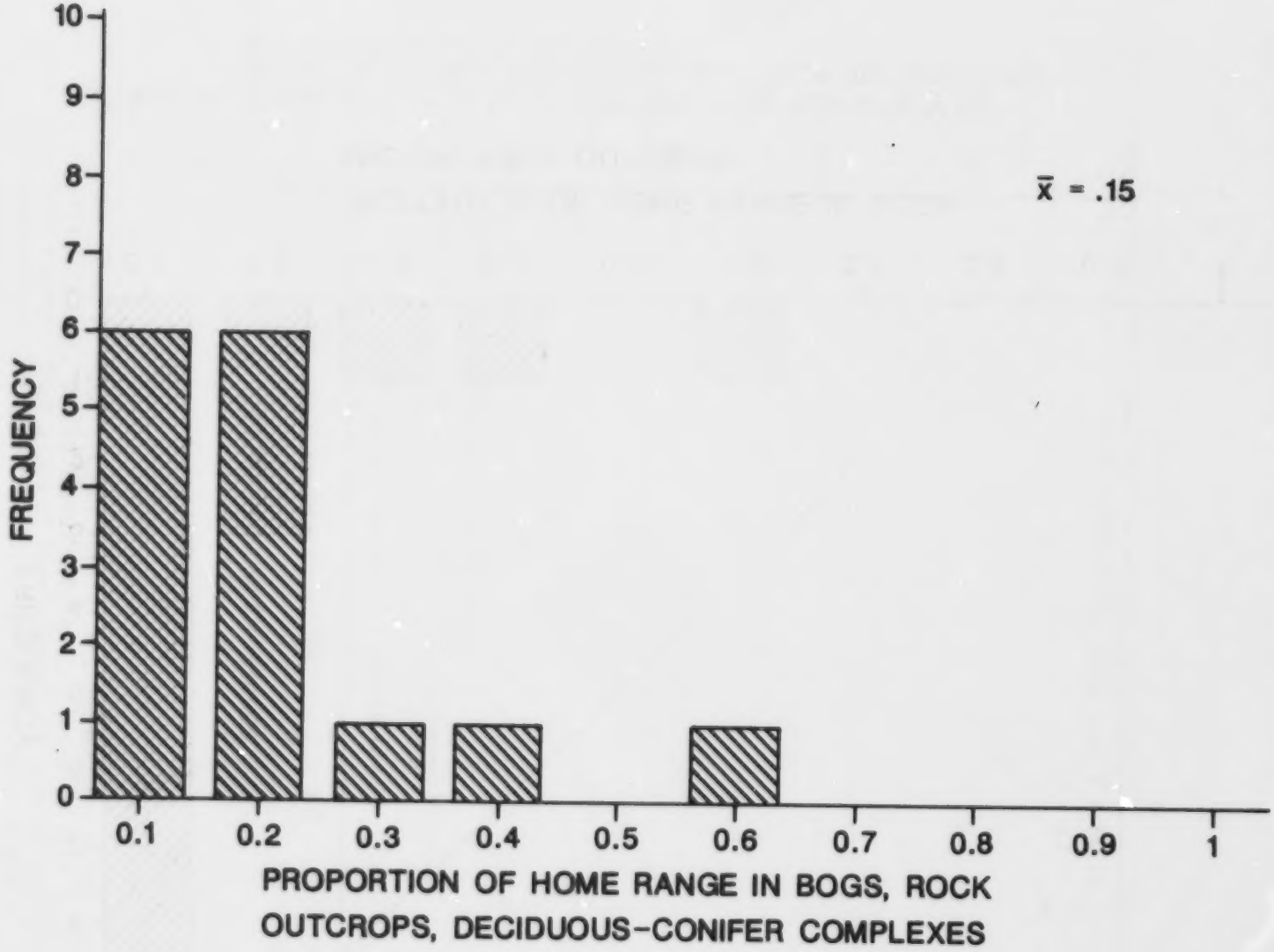

Figure 34. Frequency distribution of home range sizes from 4- to 6-day monitoring sessions based on the proportion of bogs, rock outcrops, and deciduous-conifer complexes within the home range.

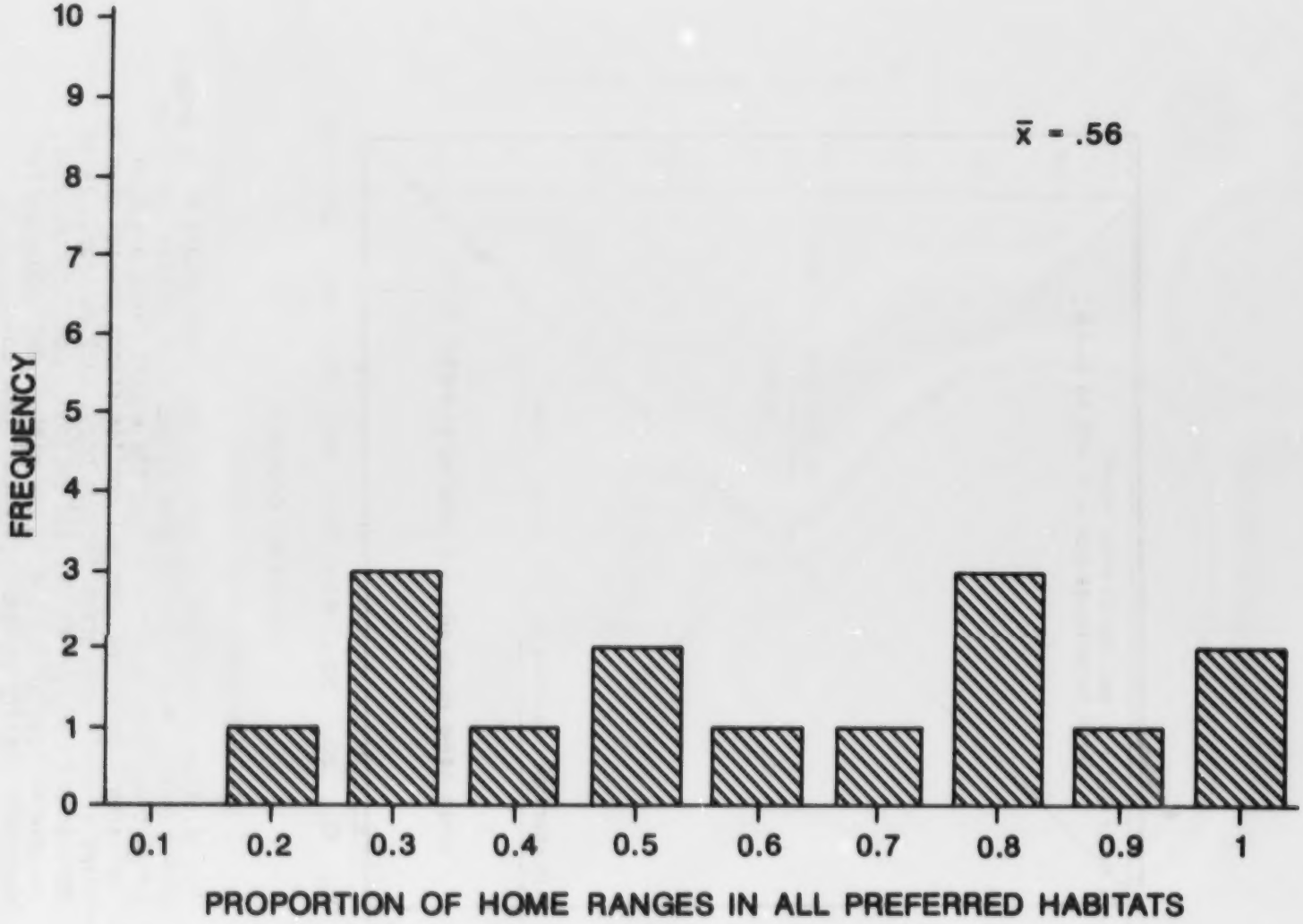

Figure 35. Frequency distribution of home range sizes from 4- to 6-day monitoring sessions based on the proportion of all preferred habitats within the home range. Preferred habitats include bogs, rock outcrops, deciduous-conifer complexes, and 21- to 60-year-old conifer stands with *Polystichum-Achlys*, *Blechnum*, and Moss-*Mahonia* ecosystem association.

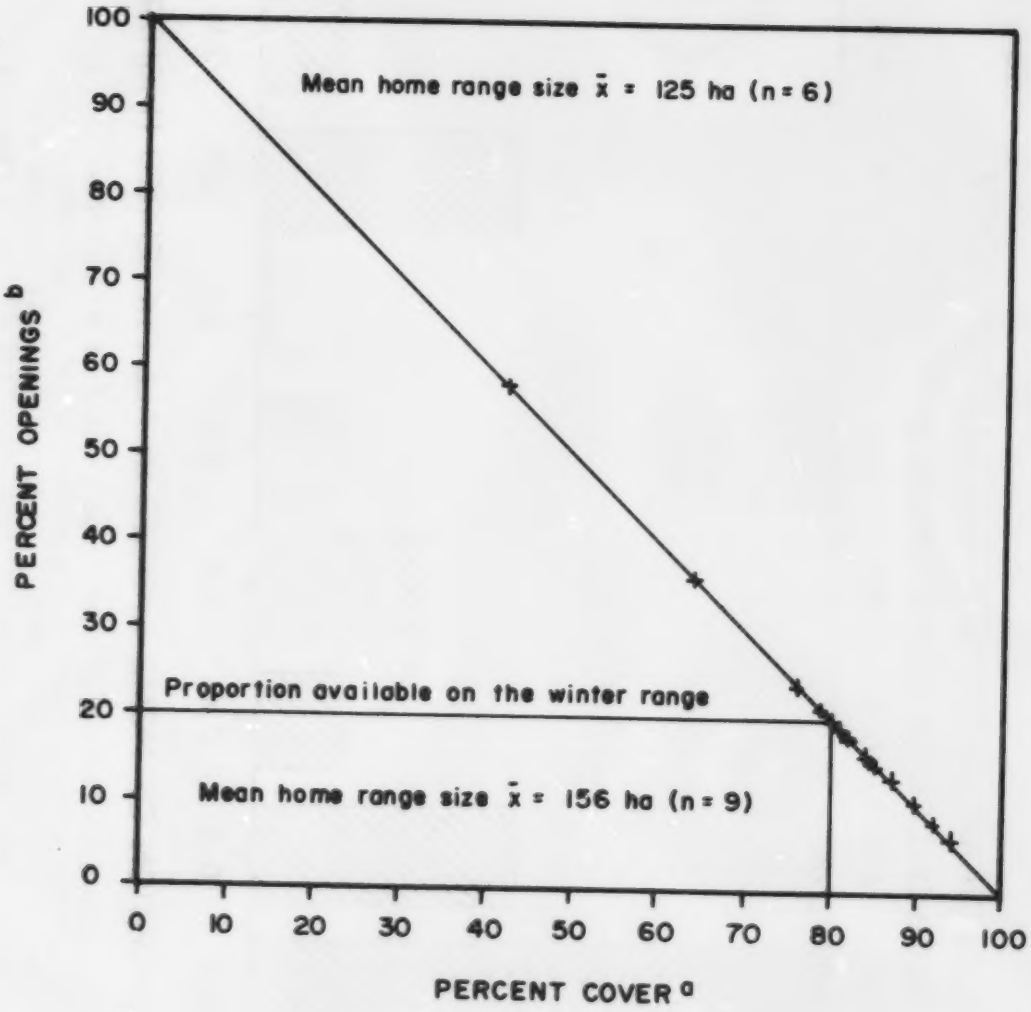

Figure 36. The relative proportions of openings and cover within 4- to 6-day home ranges. Mean sizes of home ranges with greater and lesser proportions than occurred across the winter range are also indicated. Cover includes all conifer stands greater than 20 years of age. Open areas include bogs, rock outcrops, 1- to 20-year-old conifer stands, and deciduous-conifer complexes. Because of loss of foliage in the winter, deciduous-conifer complexes qualify as openings rather than cover.

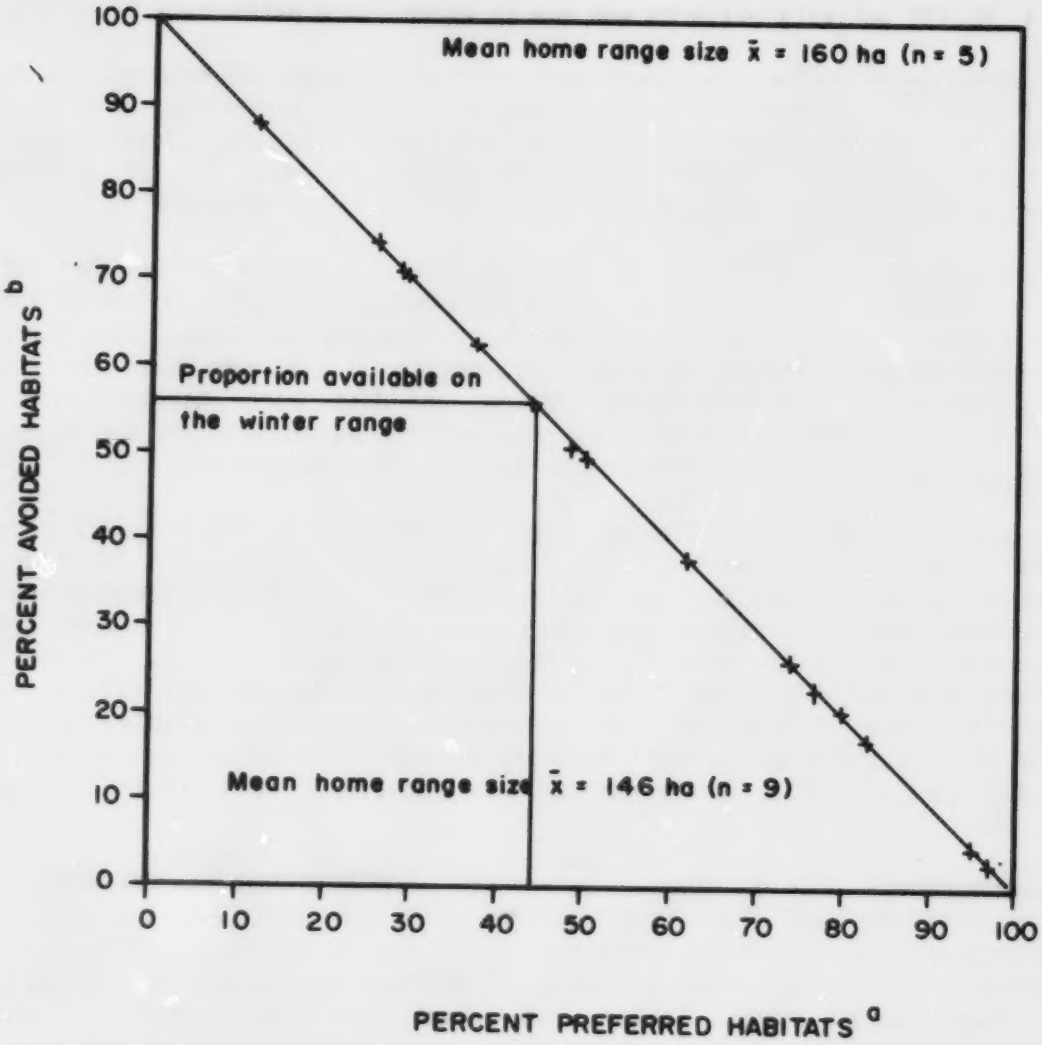

Figure 37. The relative proportions of avoided and preferred habitats within 4- to 6-day home ranges. Mean sizes of home ranges with greater and lesser proportions than occurred across the winter range are also indicated. Preferred habitats include bogs, rock outcrops, deciduous-conifer complexes, and 21- to 60-year-old conifer stands with *Polystichum-Achlys*, *Blechnum*, and Moss-*Mahonia* ecosystem associations. Avoided habitats included 1- to 20-year-old conifer stands and 21- to 40-year-old spaced conifer stands.

larger (160 ha) than home ranges with relatively less avoided habitats than available (146 ha). However, this difference was not significant ($p>.20$). A larger home range size would be expected with greater proportions of avoided habitats; smaller home range sizes would be expected when more preferred habitats were within a home range (see Section 4.7.4.1).

4.7.4.4 Winter activity patterns and energy expenditure estimates

Winter daily activity patterns were very similar in January/February 1983 and 1984 (Figure 38). Since both winters were mild, large variations in activity patterns between years were not expected. The most consistent feature was a high level of activity near sunrise and sunset. The 1 day of activity monitoring conducted in February 1985 showed similar peaks in activity.

Mean active:inactive ratios varied significantly (t-test; $p<.10$) between 1983 and 1984 (Table 52). This difference is attributable to session one in 1983 in which percent time active (57.9%) was approximately 10% higher than during any other session. During this session, monitored elk were near the road systems from which they were being located, and disturbance may have been a factor in the higher percent activity observed. Mean temperature during each session was not significantly related to percent activity ($p>.10$).

Sample sizes for percent active and inactive locations by stand type are too low for statistical comparison (Table 53). However, a trend of higher percent activity in bogs during 1983 and 1984 is apparent. Spearman rank correlations were used because the data were not normally distributed. No significant relationship ($p>.020$) was noted between percent canopy closure of the stand type in which each location occurred, and percent activity during the location hour. Spearman rank correlations between temperature at the time of each location and percent activity during the location hour were also non-significant ($p>.20$). These results were expected, given the mild winter conditions.

Estimates of daily winter energy requirements were made based on the combined mean percent time active and inactive for 1983 and 1984, and estimates of energy expenditure for elk in these activities (Gates and Hudson 1978; Parker 1983) (Table 54). Gates and Hudson used 10-month-old calves in estimating energy expenditure, whereas Parker used calves less than 4 months of age. Daily energy expenditures were estimated to range from 8834 (Gates and Hudson 1978) to 15 737 (Parker 1983) kcal for a 250-kg elk. Assuming a food value of 4.5 kcal/g for forage leaves and stems (Robbins 1983) and an average winter forage digestibility of 33% (this study), an adult female elk would require between 5.9 and 10.6 kg dry matter of forage per day for maintenance during a mild winter.

The large variation in estimated daily energy expenditures and forage requirements is probably a result of age differences in experimental animals

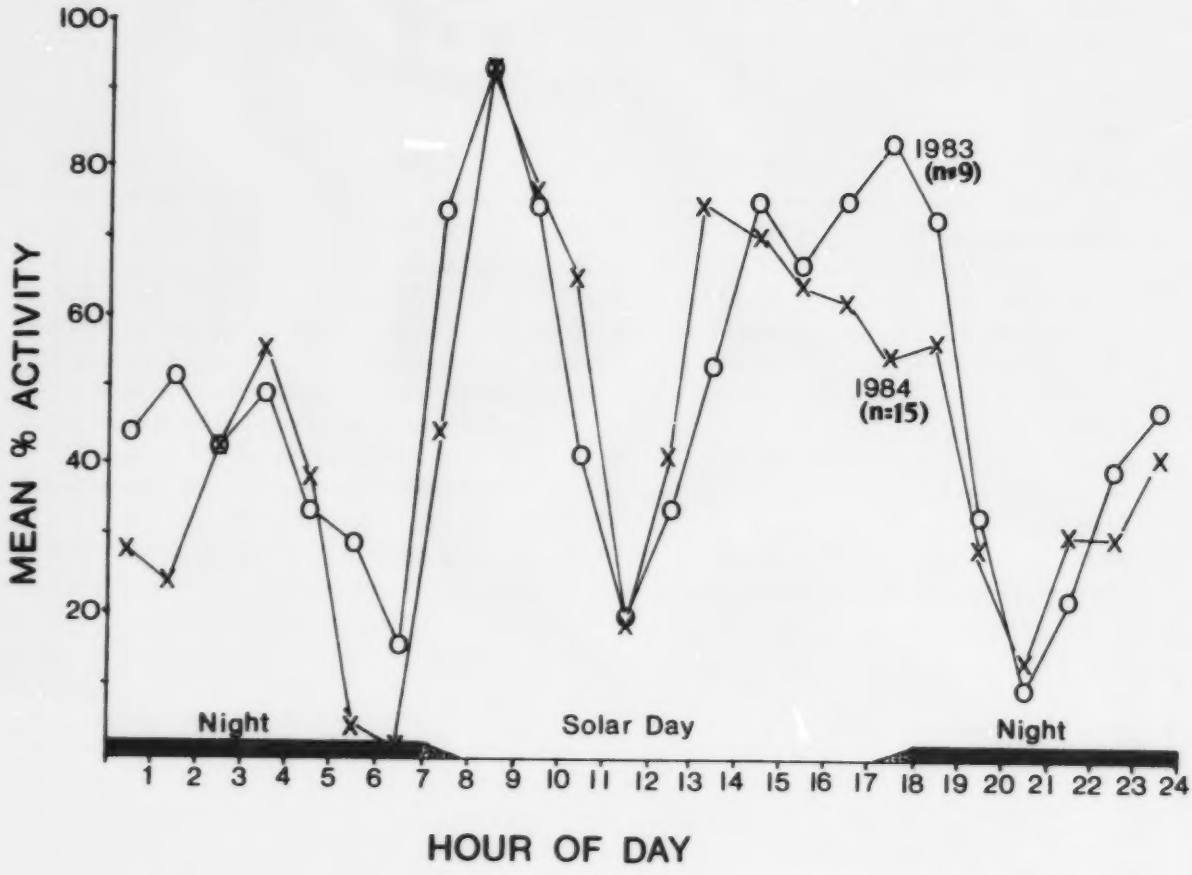

Figure 38. Mean percent activity by hour for one radio-collared elk cow in the Greenstone herd during January and February 1983 and 1984 (n = number of activity monitoring days composing sample).

Table 52. Percent of time active and inactive, mean length of activity periods, and mean temperature during each winter intensive monitoring session in 1983 and 1984

Year	Session	% Active	% Inactive	Active: inactive ratio	Mean length of activity periods (h)	Mean Temp. (°C)
1983	Jan. 25-28	57.9	42.1	1.38	1.7	4.7
	Feb.10-13	44.1	55.9	0.79	1.1	3.8
	Feb.19-22	47.0	53.0	0.89	1.2	4.7
1983 Mean		49.7	50.3	0.99	1.3	4.4
1984	Jan.10-13	42.9	57.1	0.75	0.8	---
	Jan.23-26	48.2	51.8	0.93	1.2	2.8
	Jan.31-Feb.3	43.3	56.7	0.76	1.0	1.9
	Feb.12-15	48.0	52.0	0.92	1.3	2.6
	Feb.19-22	44.6	55.5	0.80	1.6	3.4
1984 Mean		45.4	54.6	0.83	1.2	2.7
Combined Mean		47.0	53.0	0.90	1.2	3.4

Table 53. Percent active and inactive locations by stand type during the 1982/83 and 1983/84 winters

Stand[1] type	Total locations with activity recording	% Active (n)	% Inactive (n)
1	15	87 (13)	13 (2)
2	8	50 (4)	50 (4)
3	7	57 (4)	43 (3)
4	95	46 (44)	54 (51)
5	2	-- (1)	-- (1)
6	9	56 (5)	44 (4)

[1]Stand types:
1 = Non-productive forest lands (bogs and rock outcrops)
2 = Deciduous-conifer complex
3 = 1- to 20-year-old conifer
4 = 21- to 60-year-old conifer
5 = 21- to 40-year-old spaced conifer
6 = Mature and old-growth conifer

Table 54. Estimated daily energy expenditure and forage requirements of a 250-kg elk during winter. Energy expenditure estimates by activity from both Parker (1983) and Gates and Hudson (1978) are presented.

Reference	Activity	Energy expended in activity (kcal/day)	% Time spent in activity[1]	Daily energy expended (kcal/day)	Estimated forage requirement (dry matter kg/day)[2]
Parker (1983)	inactive[3]	11 718	53.0	6211	
	active[4]	20 268	47.0	9526	
			Daily totals -	15737	10.6
Gates and Hudson (1978)	inactive	6 948	53.0	3682	
	active	10 962	47.0	5152	
			Daily totals -	8834	5.9

[1]An average of winter activity monitoring data collected in this study.
[2]Based on an average dry matter forage value of 4.5 kcal/g which is 33% digestible.
[3]An average of lying and standing energy costs.
[4]An average of walking (at 2 km/h) and standing energy costs.

used in the two studies. The 10-month-old calves used by Gates and Hudson (1978) expended only about 50-60% as much energy as the 4-month-old calves used by Parker (1983) in the lying, standing, and walking modes used to develop the active and inactive energy expenditure estimates adopted for this study. Young animals would be expected to expend a larger amount of energy per unit body weight because of their generally higher metabolic rate. For this reason, the data from Gates and Hudson (1978) probably represent a more realistic estimate of energy expenditures and forage requirements for a 250-kg elk during a mild winter. During a severe winter, increased costs of thermoregulation and locomotion through snow would significantly increase energy expenditures. Similarly, fleeing from predators or human disturbance would also increase the estimated maintenance requirements presented here.

5.0 CONCLUSIONS AND RECOMMENDATIONS

Weather conditions during the study were similar to the preceding decade although winters were generally milder with minimal snow accumulations. Two of the four winters studied were classified as moderate and two as mild, based on snow depths. However, even during the moderate winters, snowpacks did not persist for extended periods and it was felt that elk were not stressed to the degree they would be during a severe winter of the type which periodically occurs on Vancouver Island. Interpretations of winter habitat use data presented here must consider that elk habitat requirements during a severe winter may differ significantly.

5.1 General Movement Patterns

At least five elk herds (two migratory and three resident) occur within the study area. Migratory elk generally occupy distinct summer, winter, and transitional (spring and fall) ranges, while resident elk occupy a single annual home range. Seasonal ranges of migratory elk herds can be extensive (>40 km^2) although individuals or groups within a herd usually use only a portion of the entire seasonal range. All portions of a seasonal range are usually available to individuals or groups, and habitat management activities within or adjacent to a herd's range may affect habitat use patterns and population performance of that herd.

5.2 Forage Areas

Seasonal habitat and forage preference analyses emphasized the importance of moist forage production areas, including bogs, riparian areas, seepage sites, and deciduous-conifer complexes. Winter home range sizes decreased as the proportion of moist habitats within the home range increased. Wet areas produce abundant preferred elk forage species, and forest management practices in and around these areas will benefit elk production if the areas' integrity is maintained or forage production is enhanced. Visual screens of vegetation or topographic barriers adjacent to open foraging areas such as bogs, clearcuts, and rock outcrops appear to enhance elk use substantially.

Site conversion of stands used as foraging areas, from a deciduous- to a coniferous-dominated overstory, may result in browsing damage to planted conifers if alternative forage is not maintained--particularly when broadcast spraying of herbicides follows the removal of the overstory. The maintenance of natural forage or provision of alternative forage through planting of preferred species may alleviate browsing damage to conifers.

5.3 Animal Condition and Diet Quality

Animal condition indices measured throughout the study indicated that elk in the area were on a relatively high nutritional plane. Estimated dietary

crude protein ranged from an average of 8.0% in winter to 17.5% in summer, while diet dry matter digestibility ranged from 45 to 59% in winter and summer, respectively. Estimated protein content of diets exceeded minimum maintenance requirements during all seasons, but digestible energy content fell below maintenance levels during winter.

5.4 Population Characteristics

Seasonal range population density estimates of migratory herds were similar for summer and winter ranges. It is likely that winter range densities would increase during a severe winter as elk concentrated in smaller areas that satisfied their requirements during deep snow accumulations.

Mean conception and parturition dates of September 28 and June 2, respectively, were determined. Pregnancy rates were 85% for cows 2.5 years of age and older in the study area and adjacent areas. These results, along with minimum estimates of 9 adult or 21 yearling and older bulls per 100 cows from classified counts in summer, suggest that enough bulls were present in the study area to carry out breeding activities. Habitat quality was apparently sufficient to maintain a reasonably high reproductive output during the relatively mild winters of the study. Analyses suggest that population levels in the study area and adjacent areas are generally increasing, probably as a result of the relatively mild winters experienced in recent years.

Estimated mortality rates of adult males were substantially higher than for adult females. Hunting (legal and illegal) and wolf predation appeared to be the main sources of mortality for adult elk. The principal factor limiting population growth appears to be calf survival. Spring calf:cow ratios generally correlated with the previous winter severity index. This suggests that winter severity is an important factor determining calf survival. During a severe winter, mortality rates of both calves and adults are expected to be substantially higher. Wolf predation may also become an important factor influencing elk population levels when wolf densities are high, during severe winters, or when deer populations are depressed.

5.5 Habitat Use Patterns

Backlog spacing debris virtually excluded all elk use. Debris depths remain impenetrable for a decade or more following treatment. Directional falling, or trailing, bucking, or removal of debris is necessary to encourage elk use of backlog spaced stands.

Calving typically occurred on benches among steeper terrain. The influence of logging activity on calving site use remains unclear, but it appears that vegetative and topographical barriers between calving areas and logging activity may reduce the impacts.

Summer range habitat use assessments indicated a preference for bogs and mixed conifer/deciduous stands because of the abundance of preferred forage species in these moist habitat types. Use of old-growth forests was high, but it did not exceed availability on the summer ranges studied where old growth is still relatively abundant.

Natural openings were preferred as foraging areas over man-made openings. During both mild and moderately severe winters, elk displayed a preference for deciduous-conifer complexes, and 21- to 60-year-old conifer stands with moister ecosystem associations. Bogs were a preferred foraging habitat in winter except during periods when snow accumulations exceeded about 30 cm. During these periods, elk often shifted their use to south-facing rock outcrops. The higher snowmelt rates on rock outcrops resulted in reduced snow depths and provided easier mobility and greater forage availability. Favourable thermal conditions were also found on south aspect rock outcrops on clear, sunny days. Clearcuts (1- to 20-year-old conifer stands) were avoided during both mild and moderately severe winters.

The availability of preferred forage species and habitats explained much of the variation in patterns of winter habitat use. Reductions in the size of home ranges were observed as the relative proportion of preferred forage species and habitats within the home range increased.

Peaks in activity were noted during early morning and late afternoon on days when elk activity was monitored during mild winters. An estimated 6-11 kg of forage dry matter was required to satisfy the daily energy expenditure of an adult elk. Elk may survive on lesser quantities of forage by using fat reserves obtained during the previous summer and fall. Overwinter weight loss is common for ungulates in temperate zones. However, during a severe winter, energy expenditures would be substantially higher and forage availability reduced by snow accumulations. This energy deficit could become severe and lead to substantial overwinter mortality in all age classes if sustenance forage does not remain accessible to elk during periods of deep snow accumulations. Old-growth forests appear to be best at providing reduced snow depths and sufficient forage during periods of substantial snow accumulations. It is suspected that overwinter mortality during a severe winter would have been substantially higher than was observed during the study because of the extremely limited amount of old growth available to elk wintering in the study area.

Elk preference for edges between open forage areas and forested cover areas was very high on all seasonal ranges. It is recommended that forestry activities be carried out to maintain a forage/cover edge within 200 m of any point on elk seasonal ranges. Forest management activities that maximize edge and create habitat mosaics of stands in many different successional stages will be the most effective in enhancing elk habitat quality and, ultimately, population performance.

6.0 FUTURE DIRECTION

The general direction of the IWIFR Elk Research Program and specific recommendations for future study are presented.

6.1 IWIFR Phase II

Agreement has been reached by the British Columbia Ministry of Environment and Ministry of Forests to extend the Integrated Wildlife Intensive Forestry Research (IWIFR) program for an additional 5 years, until March 1991. A proposal of activities to be carried out during this Phase II portion of the program has been prepared.[3]

The major goal in Phase II will be to develop further, and transfer the results of, Phase I research. Technical transfer of Phase I results to forest and wildlife managers will be accomplished mainly through the use of a handbook dealing with deer and elk habitat management in the coastal forests of southern British Columbia, which will be available in 1988.

A preliminary version of an elk habitat suitability assessment tool has been developed (Brunt and Ray 1986). This model will be tested and refined during Phase II through the comparison of predicted and actual habitat use of elk transplanted into an area previously void of elk.

Another important activity during Phase II of the program will be the development of a Habitat Assessment Procedure (HAP) dealing with the spatial and temporal arrangement of habitats across the landscape. The result will be a tool for assessing the effects of forestry practices on deer and elk habitat over time and space. A computer model will be developed, linking elk habitat requirements with forest stand development models so that the impacts of a wide variety of forest management scenarios can be assessed. The HAP system will be able to deal with any required level of scale or temporal resolution.

A major question which initiated the IWIFR program was whether or not managed regenerating forests could provide deer and elk winter ranges by approximating conditions in mature and old-growth forests currently reserved from harvesting. A preliminary report of management options for regenerating stands to enhance black-tailed deer winter range quality has already been produced (Nyberg *et al.* 1986). Phase II research will continue to refine recommendations for deer winter range creation, many of which will be applicable to elk on Vancouver Island.

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[3]Harcombe, A., and T. Baker. 1987. The Integrated Wildlife/Intensive Forestry Research Program: Phase 2 Blueprint. B.C. Min. of Environ. Parks, and Min. For. Lands, Victoria, B.C. Unpublished report.

6.2 Further Research Needs

Not all the research objectives outlined in the problem analysis prepared for this study have been satisfied (Janz *et al.* 1980). The lack of a severe winter made it impossible to document elk habitat use and requirements in an area of extensively managed second growth during a stressful (high snowfall) winter. Detailed information has been obtained on elk habitat use during several mild winters and an extensive habitat inventory has been carried out on the Greenstone herd's winter range. If a severe winter did occur during the Phase II portion of the program, it is recommended that elk habitat use information be collected to fulfill this objective of the study. Additional areas in which further research is required are outlined below:

i. A method of relating habitat suitability assessment measures to elk population performance will be required for the habitat management model to be most useful. A combination of response variables, including predicted vs actual habitat use, population characteristics from seasonal classified counts and hunter-collected samples, and animal condition indices would probably be most helpful in relating habitat conditions to elk productivity and survival.

ii. The influences of juvenile spacing on understory forage production on Vancouver Island have been examined[4], but the effects of debris resulting from these activities on elk use of an area are unclear. Spacing debris has the potential to reduce or eliminate elk use of an area. The amount of debris produced and its persistence following treatment is probably a function of tree species, size (age) at treatment, pre- and post-spaced stand density, and the type of debris treatment (if any) applied. Although backlog spacing (which produces large amounts of debris which decays very slowly) will probably be much less widespread on Vancouver Island than it was during the 1970's, juvenile spacing will likely become more common in the future. The interactions between forage response and ungulate exclusion from spacing activities require more study.

iii. During the study, numerous complaints of elk damage to conifer plantations in the study area were received. A potential solution to this problem would be to provide alternative forage in recent cutovers through seeding and fertilization, particularly in areas where preferred natural forage areas (such as bogs and riparian

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[4]Nyberg, J.B., L.D. Peterson, and L.S. Stordeur. In prep. Intensive forestry effects on Vancouver Island deer and elk forage. Job Completion Report. IWIFR-EP934.01. B.C. Min. For. and Min. Environ., Victoria, B.C.

habitats) are not abundant. Specific questions to be addressed on forage seeding of clearcuts would include:

- •Which forage seed mixtures would be most successful in different habitats?
- •Will established forage species be used by elk?
- •Will planted forage compete with regenerating conifers?
- •Will the provision of alternative forage reduce elk damage to regenerating conifers?
- •What costs would be involved?

iv. More extensive aerial surveys of Vancouver Island elk populations will provide concise information on the current distribution and abundance of elk, as well as on the influences of winter severity and wolf predation on population performance.

v. The process of site conversion from deciduous to coniferous overstory is becoming an increasingly common forestry practice on Vancouver Island. The influence of this activity on elk habitat use, forage production, and conifer damage requires further research. Where extensive herbicide use is associated with these activities, the loss of heavily used forage-producing areas could strongly affect elk population characteristics and patterns of habitat use.

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APPENDIX 1. Selection indices

Selection indices were utilized to investigate habitat preference by elk as use was not proportional to availability (see Section 4.7). Habitat use is considered to be selective if habitats are used disportionately to their availability. Preference for a particular habitat is a reflection of the likelihood of that component being selected if it were offered on an equal basis with others (Johnson 1980). To determine if preference or selection for a specific habitat exists, selection indices are often used to offset the bias involved in unequal availabilities of habitats.

Determining the existence of habitat selection or preference is important, as preferred habitats may require particular management practices if elk use of an area is to be maintained. Enhancement of preferred habitats may increase elk use and/or population levels in an area.

Preference for a habitat cannot be determined on the basis of use alone. Habitat selection may be occurring in a density dependent manner. At or near carrying capacity, habitat use is likely to be linearly related to habitat value (Rosenzweig and Abramsky 1985). Since animals in the study area were not assumed to be near carrying capacity, it is reasonable to assume that selection existed.

Selection values represent availability or unavailability of habitats (or food items), as well as an actual preference or avoidance (Strauss 1979). An animal may prefer a specific habitat but that habitat may be inaccessible. Different levels of selection are also important in determining what is preferred or avoided by an animal. Simply defining what is available to an animal may be a problem. Many studies define availability as all habitats within an animal's home range (either seasonal or annual). This may result in an entire watershed being classified as available although it may be physically impossible for the animal to access some habitats. Johnson (1980) points out that whatever conclusions are reached about the preference or avoidance of a specific habitat depends upon the array of habitats deemed by the investigator to be available to the animal.

Multi-level analyses of habitat preference which may help overcome potential problems encountered in determining both abundance and availability should be employed. For example, Smith (1986), in studying habitat use of mountain goats (*Oreamnos americanus*), used two levels of selection. The first level represented the gross selection of an overall home range from the general study area. The second level of selection was based on seasonal use of specific proportions of a home range. It was implicit in these assumptions that the study animals were capable of traversing the entire

study area and that their failure to use distant portions of the study area was based on choice rather than a lack of awareness of the area.

Selection indices are usually based on the form or proportion of the resource used divided by the proportion that is deemed available to the animal. Rare habitats are often found to be preferred, and even though a habitat is used in proportion equal to its availability, this type of analysis will not identify it as preferred. Other selection indices have modified this basic equation (e.g. Ivlev 1961; Jacobs 1974), but problems still occur with unequal habitat availability. A commonly used statistical method (Neu *et al.* 1974) involving chi-square and Bonferroni Z statistics does not produce different results. A habitat type must be used more than its availability to be classified as preferred. The Bonferroni Z statistic is essentially a chi-square test of Ivlev's electivity constant. Another consideration is that preference is only reflected in selection when a component is rare. An abundant habitat might only be used in small amounts to satisfy requirements. Use of a particular habitat might be less than availability but conclusions that the habitat is of little value to the animal may not be realistic.

Johnson (1980) used a ranking approach. However, if a habitat is abundant and most frequently used, it may not be classified as preferred, depending upon the ranking of the other habitats. Chesson (1983) suggests a prey selection index that tries to assess the proportion of a food item that would be in a diet if all were equally abundant, but problems arise in attempting to use this for habitat selection in areas of unequal availability. Strauss (1979) assesses reliability estimates for both Ivlev's electivity index and the forage ratio, and shows that statistical reliability is dependent on abundances and relative sample sizes. He proposed a linear index for food selection which avoids most of the statistical and mathematical inadequacies of the earlier mentioned indices. Although there is still bias with unequal habitat availability, this method appears to minimize many of the problems associated with selection analyses.

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